

An annotated checklist of bumble bees with an analysis of patterns of description (Hymenoptera: Apidae, Bombini)

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SYNOPSIS. Bumble bees are among the minority of groups of organisms for which there is some evidence that most species have already been described. Nonetheless, a synoptic revision of the group has been delayed, in part by the difficulties imposed by an unusually high ratio of names to species (averaging more than 11). To explore some of the factors contributing to this phenomenon, historical and geographical trends in the naming of bumble bees are summarised. This shows that most taxa were named by European authors, beginning with the most widespread European species, moving later to not only the more narrowly distributed species and to species from other parts of the world, but also to taxa at progressively lower nomenclatural ranks, particularly within the more widespread European species. Nearly half of all of these names have been published since the last world-wide checklist in 1922. In attempting to bring this up to date, the present checklist adopts broad interpretations of species and recognises a total of 239 recent species (including the social parasites but excluding fossil taxa), with 24 new synonyms and 29 provisional synonyms. The list also includes notes on alternative interpretations of taxonomic status and on nomenclatural problems, drawing attention to those cases where further research is most urgently needed. In particular, suggestions are presented for an application to the International Commission on Zoological Nomenclature to use its Plenary Power in order to conserve current usage of the commonly used names *atratus*, *balteatus*, *distinguendus*, *flavifrons*, *humilis*, *hyperboreus*, *mesomelas*, *mixtus*, *norvegicus*, *polaris*, *pyrenaicus*, *soroeensis* and *variabilis*.

INTRODUCTION

Bumble bees have long been popular with collectors. Just as with butterflies, part of the attraction may be explained by their bright colours, large body size, activity during daylight hours, and abundance in the north-temperate regions where most collectors have lived. As a result, large samples of bumble bee specimens have now been assembled, even from remote parts of the world.

A problem for biologists trying to identify bumble bee species, all the more apparent because of the large amount of material available, is that while bumble bees can be described as morphologically relatively 'monotonous' (Michener, 1990), they are often extraordinarily variable in the colour patterns of their pubescence. The situation is made worse by a strong tendency for species to converge locally on different colour patterns (Plowright & Owen, 1980).

Faced with this variation, generations of taxonomists since the starting point of Linnaean nomenclature in 1758 have described differing individuals under a plethora of more than 2800 formal names (Williams, unpublished catalogue, including names for species, subspecies and synonyms, as well as infraspecific names, misspellings and other unavailable names). Most of these names are for taxa below the rank of species, and just 239 taxa are interpreted here as separate species. Arguably, the nomenclatural burden of more than 11 names per species (median 5, maximum 186) has slowed progress towards a complete revision of the group. Hence there is a need for an overview which, although bound to require revision, will provide an improved framework for more detailed regional studies. It is also important to understand any regional or taxon-directed bias in patterns of taxonomic description when seeking to interpret patterns in diversity, ecology and biogeography. The present checklist begins to address these needs.

Past lists of species

There have been few attempts to present complete revisions, catalogues or checklists of all bumble bee species from which to see summaries of past views. Latreille (1809) included 13 species in his genus *Bombus*. Most of the early lists included just those species seen by their authors, usually from particular collections, and often from just one region. For example, Smith (1854) catalogued 87 bumble bee species (79 *Bombus* + 8 *Apathus* [= *Psithyrus*]) in the collection of the British Museum. The only truly synoptic catalogue of bumble bees was published by Dalla Torre (1896), with 255 (non-fossil) species (228 *Bombus* + 27 *Psithyrus*). It included many varietal names, synonyms and early references. The reason

why Dalla Torre's species count exceeds the total now recognised as described before 1899 (159 species, Fig. 1) is of course that many of his species are now treated as synonyms or subspecies. Later, Skorikov (1922a) listed 237 species (plus 70 '*Bombi incertae sedis*'), but with few synonyms and without including *Psithyrus*. Nonetheless, Skorikov's list did arrange most of the known species within his genera and subgenera, which form the basis of the current subgeneric system (Richards, 1968).

Taken together, the few past lists of bumble bees show that the number of taxa accepted as species at a particular date grew rapidly during the nineteenth century, but has since remained relatively stable, with a slight decline to the conservative estimate of 239 species in the present list. Undoubtedly part of the explanation for this decline lies in the relatively conservative species concept accepted at present (see below). This reflects a gradual shift in emphasis among criteria for recognising species from the use of colour characters to the use of morphological characters, particularly to using characters of the male genitalia (see the introductory comments by Radoszkowski, 1884). A similar pattern of growth and decline has been found for past numbers of milkweed butterfly species (Ackery & Vane-Wright, 1984). However, there might now be another period of rapid growth if molecular characters and phylogenetic species concepts (discussed below) were to be applied (cf. discussion of the number of bird species by Martin, 1996; Patterson, 1996; Zink, 1996, 1997; Snow, 1997).

History of discovery of species

The dates of first formal description for the currently recognised bumble bee species show that the highest rates of species discovery were in the latter half of the nineteenth century through to the First World War (Fig. 1, median date 1877). These species are recognised retrospectively from the present list, rather than as the numbers accepted within each time period. The larger dips in overall rate of discovery may be associated with factors such as war and its aftermath (e.g. Napoleonic and Second World Wars), presumably through constraints on resources and on freedom of travel.

Some authors described many more bumble bee species than others: 45% of presently accepted species were described by just 10% of the authors who described these species (Smith 32 species, Skorikov 19, Cresson 17, Morawitz 15, Radoszkowski 13, and Friese 12). Similarly, Gaston, Scoble & Crook (1995) found a skewed pattern of activity among authors describing geometrid moths. But of the six authors who described the most bumble bee species, only Ezra Cresson (Snr) actually worked in the New World, whereas the other five were based in Europe (including European Russia).

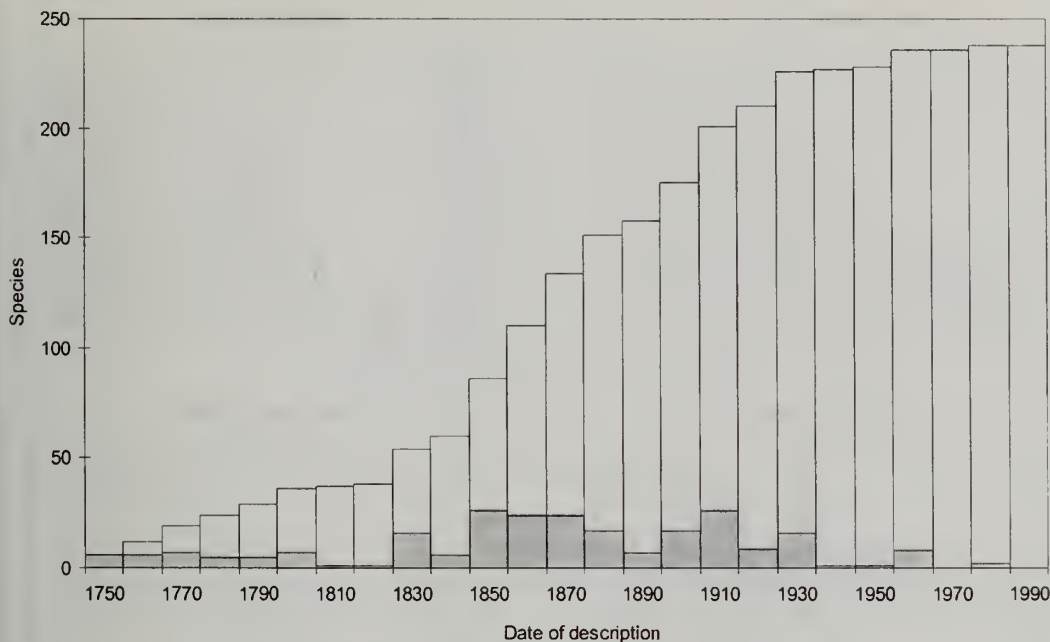


Fig. 1 Rate (lower grey) and cumulative number (upper white) of first formal descriptions of presently recognised bumble bee species (dates from the oldest available names in the sense of ICZN, 1985).

Rates of discovery of bumble bee species vary to some extent among biogeographic regions (Fig. 2). Again, this was also found for geometrid moths by Gaston, Scoble & Crook (1995). For bumble bees, the recent proportional discovery rates have been lowest in the New World and highest in the Oriental Region. The Neotropical Region appears to have a small known bumble bee fauna for its large area. There is no obvious evidence that descriptive effort has been lacking, although detailed revisionary work is needed and species with small range sizes may remain to be discovered. In contrast, the Oriental Region's high recent proportional rate of species discovery, despite its smaller area than the other regions, is possibly explained in part because it has been studied intensively for a shorter period.

The world-wide rate of discovery of genuinely unknown bumble bee species appears now to be slowing down (Fig. 1). Undiscovered species are very likely to remain, although there is no evidence that large numbers of species are awaiting description in collections (although some known subspecific taxa might yet be recognised as species if changes were to occur in species concepts or in the availability of character evidence, see Martin, 1996; Patterson, 1996; Zink, 1996). The sigmoidal pattern of species discovery in Fig. 1 is also shown by a few other relatively well known groups such as birds, although for most large groups (including Hymenoptera as a whole) the rates of description continue to be high or are even increasing (Hammond in Groombridge, 1992; Tennesen, 1997).

History of publication of names

The present checklist is intended only to address the question of taxa at the rank of species (see below). For this purpose it is not necessary to consider concepts of taxa at the rank of subspecies and below and subspecific names may be treated in analyses as further synonyms of species (Gaston & Mound, 1993). This is not to say that subspecific taxa ought not to be recognised if they were considered useful in the context of other studies. In addition, some authors have applied classical names to taxa at even lower nomenclatural ranks, for example in referring to 'varieties' or 'forms' within subspecies. These are now interpreted as infrasubspecific names and are 'unavailable' for use in the sense of the *International Code of Zoological Nomenclature* (ICZN, 1985). They have had to be included in a manuscript catalogue (unpublished) in order to avoid confusion by explicitly resolving questions of nomenclatural status and availability. Infrasubspecific names are included in this analysis as a category separate from specific or subspecific names because of their particular significance for understanding historical patterns in the description of diversity at the lowest nomenclatural ranks.

Bumble bees have the highest known levels of synonymy (83%, or 92% if infrasubspecific names were to be included) in comparison with the range of insect taxa reviewed by Gaston & Mound (1993). Their results showed synonymy levels ranging from 7% for Siphonaptera to 80% for Papilionidae and

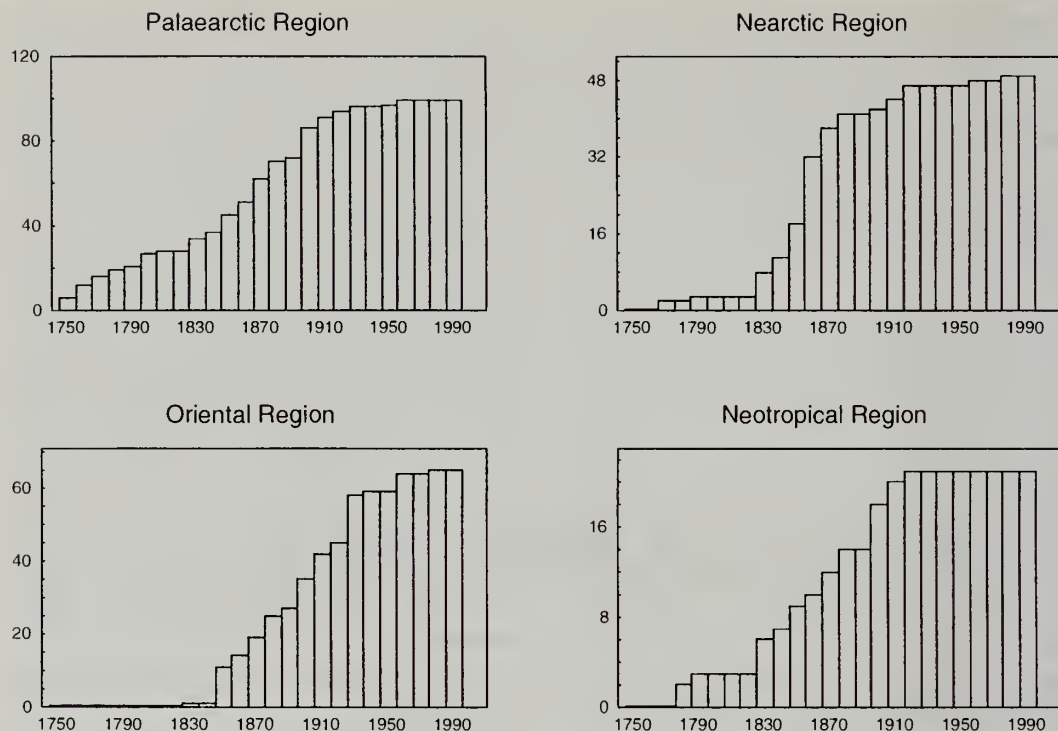


Fig. 2 Cumulative number of first formal descriptions of presently recognised bumble bee species with centres of area of occupancy (so species lists do not overlap) in each of the four principal biogeographic regions occupied by bumble bees (dates from the oldest available names in the sense of ICZN, 1985; regions defined in Williams, 1996b: fig. 1; Oriental includes northern and southern Oriental Regions; Nearctic includes northern, central and southern Nearctic Regions; Neotropical includes northern, central and southern Neotropical Regions; the Arctic Region is excluded; species that are exclusively peri-Tibetan Oriental but which nevertheless have range centres in Palaearctic central Tibet by simple range averaging are included as Oriental species).

Pieridae combined. It must be born in mind that the insect taxa that they surveyed are all more speciose than the bumble bees by a factor of at least four, and extreme values for larger groups are less likely. Nonetheless, Gaston & Mound (1993) also noted that the two families of most brightly coloured butterflies have the highest levels of synonymy and that these families have many more subspecific names than the smaller and duller-coloured hesperiid butterflies. R. I. Vane-Wright (pers. com.) suggests that synonymy rates may be particularly high among the large, colourful butterflies of the Danainae and *Parnassius*.

In contrast to the discovery of currently recognised species, the greatest activity in publishing names for all supposed bumble bee taxa at the rank of species and below was concentrated slightly later than for presently recognised species, in the first half of the twentieth century (Fig. 3, median date 1922). This difference may be explained in part by the logical inevitability that synonyms and names for taxa below the rank of species can only be published subsequently to valid

species names (i.e. the oldest available names, excluding junior homonyms, in the sense of ICZN, 1985). If these names were in effect to represent the redescription of known species at random, then the earlier described species might be expected to have accumulated more names. Studies of other taxa have also shown that both the date of first description and the number of synonyms per species may be affected by variation in the size of a species' geographic range (as well as by other factors such as body size). Large range size is likely to affect the date of first description because it contributes to a greater 'apparency' of the species to collectors (Gaston, Blackburn & Loder, 1995), particularly as broad correlations between range size and abundance suggest that widespread species also tend to have higher local densities (Brown, 1984; Gaston, 1994; for bumble bees, see Hanski, 1982; Williams, 1988). Apart from enhancing the chances of random redescription, large range size is also likely to affect the number of synonyms because there is a greater likelihood that specimens collected in one area will be regarded as

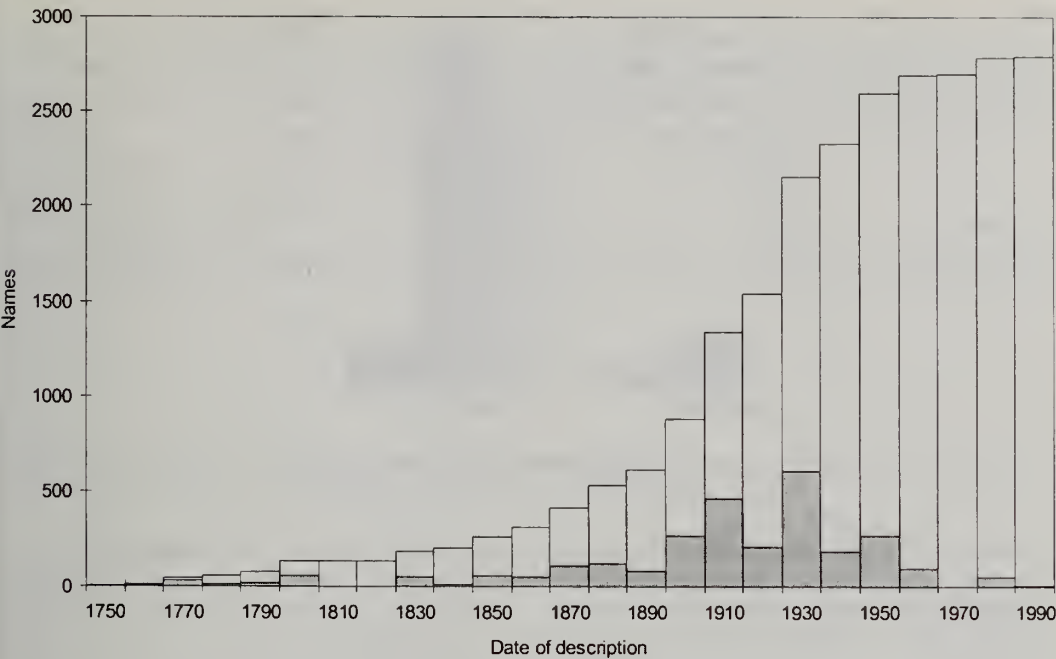


Fig. 3 Rate (lower grey) and cumulative number (upper white) of all descriptions with classical names for bumble bee species, subspecies and infrasubspecies since the starting point of zoological nomenclature in 1758 (from a manuscript catalogue, unpublished).

distinct from specimens collected from another distant area, because character variation is apt on average to be greater (Gaston, Blackburn & Loder, 1995).

For the bumble bee catalogue data, the number of synonyms (including subspecies, but excluding infrasubspecies) is correlated with both the date of first description and the range size of a species independently of one another, although slightly more of the variation is explained by variation in range size (partial r , Table 1). Many of the species with large range sizes, early dates of first formal description and many synonyms are found in western Europe (i.e. triangles at the left and upper part of Fig. 4). Most of these species occur in either the lowland areas of Europe where early naturalists were most active, such as Britain, or else are nearly circumpolar in their distribution.

Curiously, all of the infrasubspecific names (34% of all names as interpreted at present) belong to the bumble bee species of the Old World (Fig. 5). Species of the Old World also have more synonyms and subspecies per species than do the species of the New World (numbers of names log-transformed and excluding 6 Holarctic species, $t_{232} = 3.81$ with separate variance estimates, $p < 0.001$).

One possible explanation for the greater numbers of names per species for bumble bees of the Old World is that they might have broader distributions

than the species of the New World (see above). This could arise because the Old World has a slightly larger total area of suitable habitat (bumble bees occupy 131 of the 611,000 km² grid cells in the Old World and 117 in the New), which is apparently subdivided into fewer well differentiated biogeographic assemblages of bumble bee species (e.g. Williams, 1996b: fig. 1). However, this explanation is not strongly supported by the bumble bee data, which show the difference in range sizes between the two hemispheres to be not significant, (range sizes log-transformed and excluding 6 Holarctic species, $t_{232} = -1.24$ with separate variance estimates, $p = 0.22$). Consequently, while an effect of differences in habitat area will deserve future consideration, other effects are likely to be more important.

A second possibility is that whereas bumble bee taxa of uncertain rank may have tended to be regarded more often as subspecies in the Old World, in the New World they may have tended to be regarded as species (see the discussion below of criteria to recognise species). While this factor could have contributed to the observed patterns, it is unlikely to explain why (at a lower rank) so many infrasubspecific names were described exclusively for taxa from the Old World.

A third possibility is that the diversity of languages used for taxonomic publications in the Old World may

Table 1 Results of multiple regression of numbers of synonyms/subspecific names (infrasubspecific names are excluded; from a manuscript catalogue, unpublished) on date of first formal description for presently accepted species and range size (number of occupied 611,000 km² grid cells world-wide). Partial *r* values indicate the correlations with the synonyms variable after adjusting for the other predictor variable in each case.

$\log_{10}(\text{synonyms}+1) = 6.316(\pm 0.969) - 0.003(\pm 0.0005) \cdot \text{date} + 0.401(\pm 0.057) \cdot \log_{10}(\text{range})$			
	multiple $r = 0.72$	$F_{(2,236)} = 129.76$	$p < 0.0001$
	partial r	t_{236}	p
date	-0.390	-6.51	< 0.0001
$\log_{10}(\text{range})$	0.418	7.08	< 0.0001

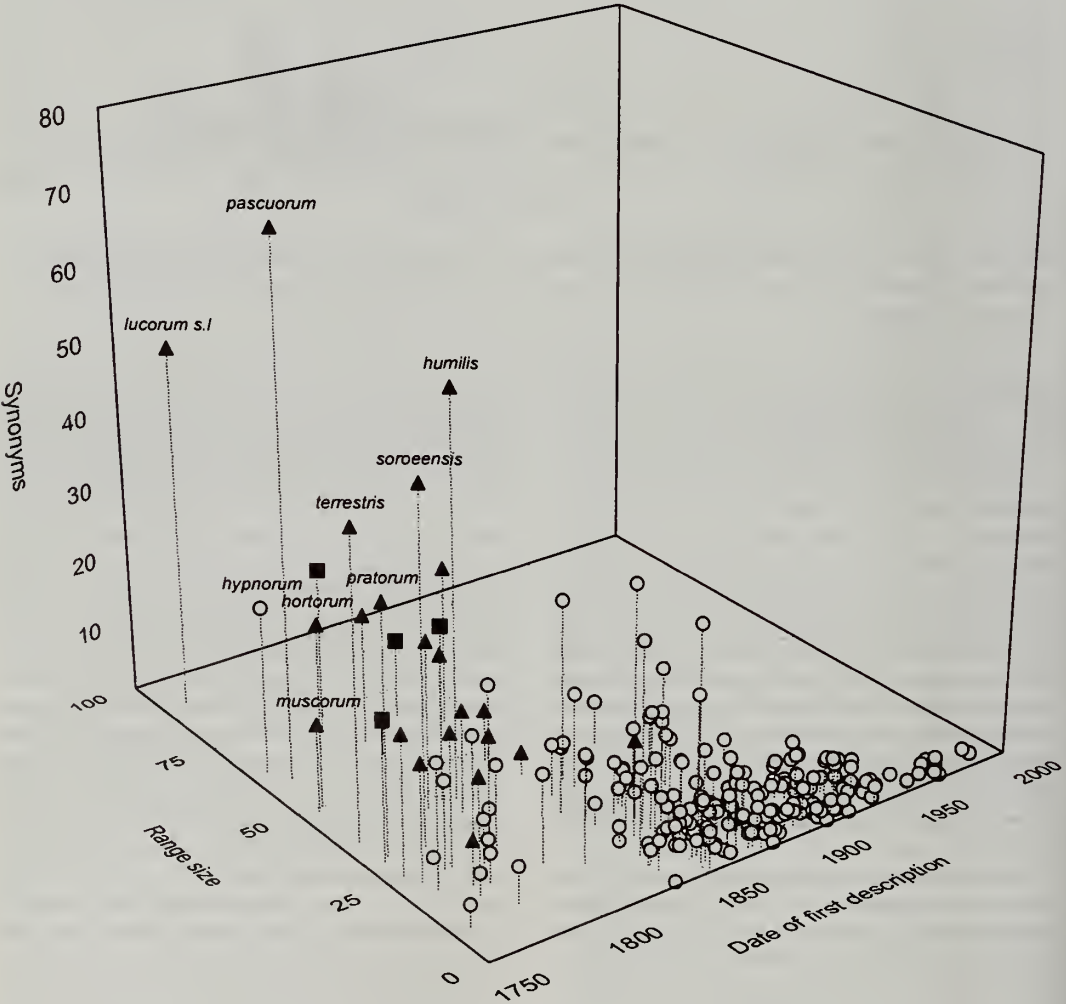


Fig. 4 Scatterplot of 239 presently accepted bumble bee species by range size (number of occupied 611,000 km² grid cells world-wide), date of first formal description and numbers of synonyms/subspecific names (infrasubspecific names are excluded; from a manuscript catalogue, unpublished). The British fauna is distinguished as filled triangles, the nearly circumpolar fauna (*B. hyperboreus*, *B. balteatus*, *B. polaris* and *B. lapponicus*) as squares, and some British and widespread European species are labelled individually.

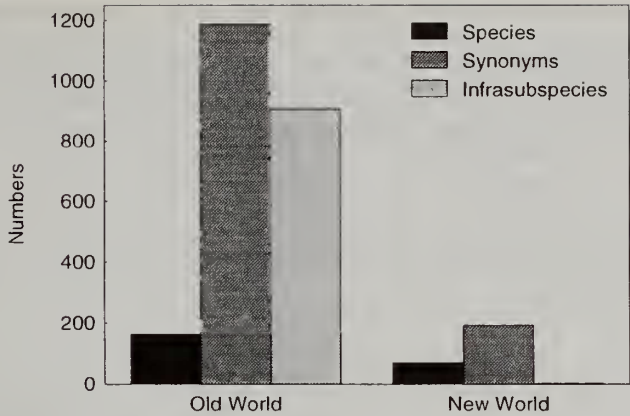


Fig. 5 Number of presently recognised bumble bee species, synonyms/subspecific names and infrasubspecific names for the Old World and the New World (from a manuscript catalogue, unpublished).

have impeded communication and lead to more frequent re-description of taxa than in the New World, where English was much more dominant (C. O'Toole, pers. com.). Again, while this factor is likely to have contributed to the observed patterns of synonyms, it does not explain why (at a lower rank) so many infrasubspecific names were described exclusively for taxa from the Old World.

Another possible interpretation, which might explain more of the differences in description dates between Figs. 1–3 as well as the differences in the distribution of bumble bee subspecies, synonyms and infrasubspecific names between hemispheres (Fig. 5), is that during the twentieth century, effort for describing the variety of these insects may have become, in effect, re-directed towards finer distinctions and lower nomenclatural ranks within known species. This is perhaps likely as undescribed species became inevitably more difficult to find close to home for the most active taxonomists, who were based in Europe. Three lines of evidence are consistent with this explanation. First, slightly more of the variation in richness of infrasubspecific names among species is accounted for by variation in the date of first description of the species (partial r , Table 2), rather than by variation in total range size. This is in contrast to the pattern for synonyms alone (cf. Table 1), although species that are sufficiently widespread in lowland Europe to include Britain within their distributions still tend to have high numbers of both synonyms and infrasubspecific names (Fig. 6, e.g. *B. pascuorum*, *B. lucorum*). A second intriguing observation is that compared to the number of authors who have published presently accepted species names, only one third the number of authors (20) have published infrasubspecific names, even though there are nearly four times as many infrasubspecific names. Indeed, just three of these authors (Bruno Pittioni, Edgar Krüger and Alexander

Skorikov) are responsible for 70% of the infrasubspecific names (all of the species with many infrasubspecific names had been described before these three authors became active in publishing infrasubspecific names between 1910 and 1960, see Fig. 7). Many similar examples are known from work on butterflies (R. I. Vane-Wright, pers. com.), with authors choosing a particular favoured species and describing large numbers of infrasubspecific names (e.g. Bright & Leeds, 1938). The third point is that the three most prolific authors all worked in Europe, and there is a correlation among all 239 bumble bee species between the number of infrasubspecific names and the breadth of the species' distributions just within Europe (measured as the number of occupied 611,000 km² grid cells between Britain and the Urals, but excluding Atlantic islands, North Africa, Turkey and the Caucasus; Spearman $r = 0.67$, $t_{237} = 13.99$, $p < 0.001$). Thus, a high proportion of the many infrasubspecific names were published by very few European authors, for previously described species that are also particularly widespread in Europe.

High numbers of synonyms and infrasubspecific names for *B. terrestris* and *B. lucorum* (subgenus *Bombus*) and for *B. humilis* and *B. pascuorum* (subgenus *Thoracobombus*) in Fig. 6 raise the possibility that large numbers of names are associated with particular groups of species, perhaps with particular subgenera. Number of names per species is plotted against range size per species for subgenera in Fig. 8. These properties are correlated (log-transformed data, correlation $r = 0.58$, $F_{1,36} = 18.16$, $p < 0.001$), but it is the subgenera with high scores that are more informative. The subgenus *Kallobombus* includes many names, but only a single, very variable species *B. soroensis*, which is broadly distributed in Europe (see below and Reinig, 1939; fig. 10). The subgenera *Alpinobombus* and *Laesobombus* also have broadly distributed

Table 2 Results of multiple regression of numbers of infrasubspecific names (from a manuscript catalogue, unpublished) on date of first formal description for presently accepted species and range size (number of occupied 611,000 km² grid cells world-wide). Species without infrasubspecific names were excluded from the analysis. Partial *r* values indicate the correlations with the infrasubspecific names variable after adjusting for the other predictor variable in each case.

$\log_e(\text{infrasubspecifics}+1) = 14.169(\pm 3.638) - 0.007(\pm 0.002) \cdot \text{date} + 0.742(\pm 0.212) \cdot \log_{10}(\text{range})$			
	multiple $r = 0.66$	$F_{(2,94)} = 36.57$	$p < 0.0001$
	partial r	t_{94}	p
date	-0.364	-3.79	< 0.001
$\log_{10}(\text{range})$	0.340	3.50	< 0.001

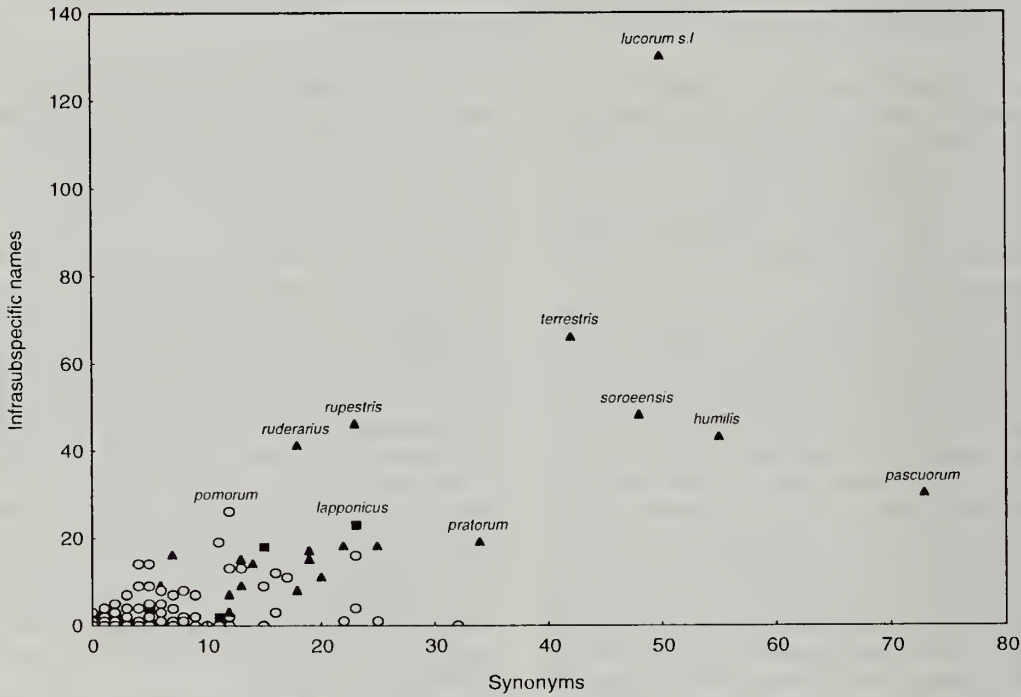


Fig. 6 Scatterplot of 239 presently accepted bumble bee species by numbers of infrasubspecific names and numbers of synonyms/subspecific names (from a manuscript catalogue, unpublished). The British fauna is distinguished as filled triangles, the nearly circumpolar fauna (*B. hyperboreus*, *B. balteatus*, *B. polaris* and *B. lapponicus*) as squares, and some widespread European species are labelled individually.

species but relatively few names, perhaps because they are absent or not abundant in those parts of Europe where the authors publishing most bumble bee names have worked, despite several of the species being very variable in colour pattern (e.g. *B. balteatus*). In contrast, the high ratio of names per species for the subgenus *Bombus* shows the keen interest by some European authors such as Krüger (1951, 1954, 1956, 1958) in describing the finer points of variation, not so

much within the North American species, but particularly within the widespread European species, *B. terrestris* and *B. lucorum*.

Summary of historical and regional trends in describing bumble bees

Based on the evidence of asymptotic tendencies in species-discovery curves, a higher proportion of all

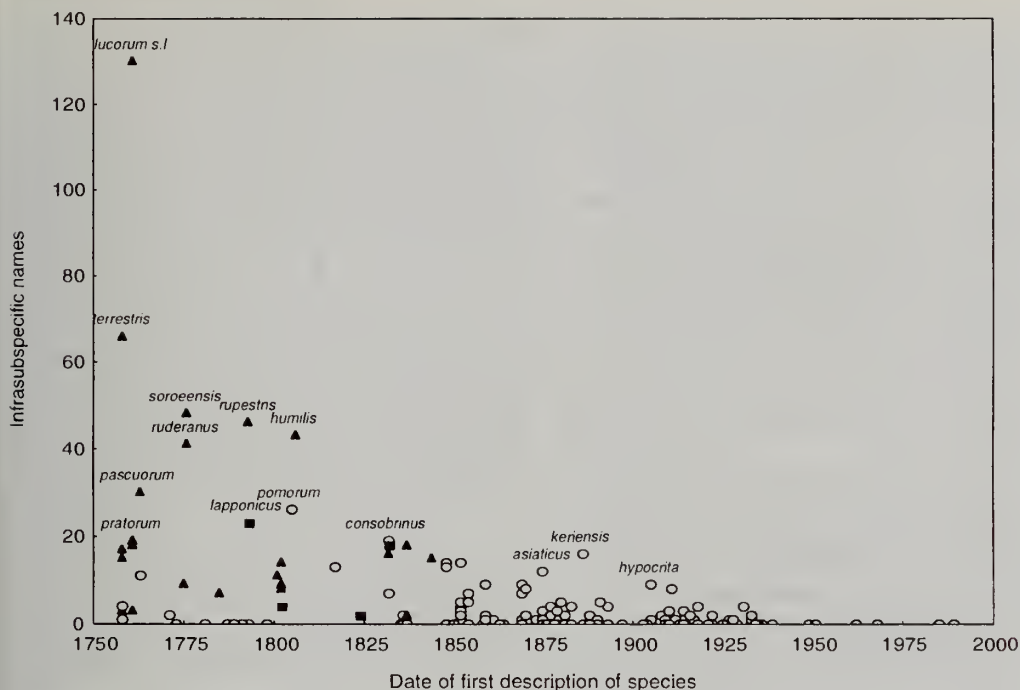


Fig. 7 Scatterplot of 239 presently accepted bumble bee species by numbers of infrasubspecific names (from a manuscript catalogue, unpublished) and date of first formal description of species. The British fauna is distinguished as filled triangles, the nearly circumpolar fauna (*B. hyperboreus*, *B. balteatus*, *B. polaris* and *B. lapponicus*) as squares, and some species with more infrasubspecific names are labelled individually.

species appear to be known for bumble bees than for many other groups of organisms. Most of these bumble bee species have been described by authors working in Europe (including European Russia). The species with the largest geographic range sizes, and particularly the European species with the largest ranges, have tended to be described first. The same species have also attracted the highest numbers of synonyms and subspecific names. As a group, bumble bees have an unusually high ratio of synonyms and subspecific names per species, which is otherwise known for some of the groups of larger and more colourful butterflies.

A few European authors were disproportionately prolific between 1910 and 1960 in describing finer variation at infrasubspecific rank, which now accounts for one third of all bumble bee names. Again, this more detailed effort has been largely concentrated on the earlier-described species that are more widespread within Europe (in contrast, New World bumble bees have been ignored at this level), presumably because large samples were more readily accessible to the most active authors. Determining whether this re-direction of activity towards lower nomenclatural ranks was a logical progression in the recognition of useful taxa, a fashion in taxonomic concepts, or in some cases merely a less disruptive channelling of the enthusiasm of

some authors to publish more names (the 'mihi itch'), is beyond the scope of this preliminary review.

All of these patterns in the descriptions of bumble bees must, as yet, be interpreted with caution. Much work still remains to be done on the rates of description of taxa at different nomenclatural ranks (species, subspecies, infrasubspecies), on rates of recognition of synonymy and of changes in rank, and particularly on how this activity is partitioned among different time periods, different geographic regions, different taxonomic subgroups and different authors.

Fundamental to almost all analyses are taxonomic revisions and checklists of bumble bee species. A revised checklist is now overdue, because nearly half (49%) of all names for bumble bees have been published since the last synoptic checklist (Skorikov, 1922a).

Development of a revised checklist

To begin to bring a checklist up to date, a draft was made in 1980 and first circulated for comment in 1985 (Williams, 1985a). This project was developed during a more detailed study of the west Himalayan fauna (Williams, 1991) and as part of continuing work on the large fauna of China in collaboration with Wang S.-f.

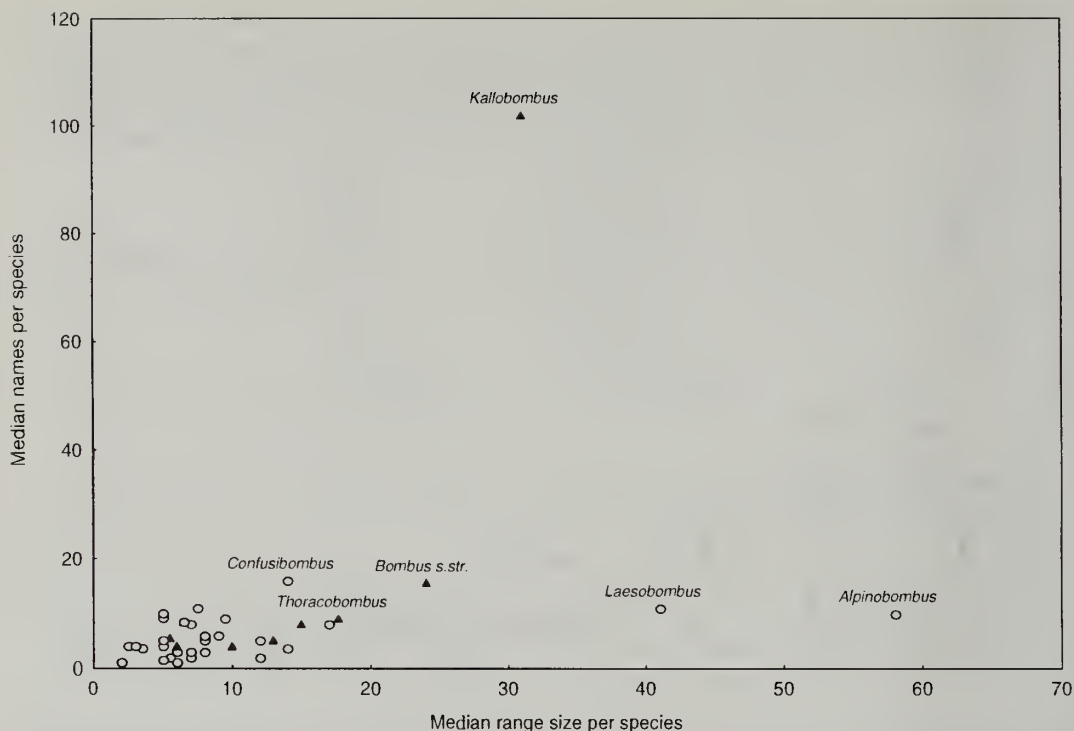


Fig. 8 Scatterplot of 38 bumble bee subgenera by median numbers of all names per species (including synonyms, subspecific and infrasubspecific names; from a manuscript catalogue, unpublished) and median range size per species (number of occupied 611,000 km² grid cells world-wide). The subgenera represented in the British fauna are distinguished as filled triangles and some subgenera are labelled individually.

and Yao J. (unpub.). Some of the broader revisions that have had the greatest influence on this include works by Vogt (1909, 1911), Franklin (1913), Stephen (1957), Milliron (1970*b*, 1971, 1973*a, b*), Løken (1973, 1984), Pekkarinen (1979), Reinig (1981), Wang (1982, 1987, 1988), Rasmont (1983, 1988), Thorp *et al.* (1983), Labougle (1990), and especially the publications by Skorikov (1910–1938) and Tkalcü (1959–1989). Inevitably, the present checklist cannot be expected to solve all biological and nomenclatural problems, but it is hoped that by identifying some of the major problems it will stimulate further research.

Acknowledgements

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Dick Vane-Wright, Doug Yanega, Yao Jian and Wang Shu-fang, although they do not necessarily share the opinions expressed here. I particularly appreciate the help of Philip Tubbs, Executive Secretary to the ICZN, for advice on the application of the current Code (ICZN, 1985) to nomenclatural problems. My thanks to Julie Harvey and Lorna Mitchell of the Entomology Library (Dept of Library and Information Services, NHM) for all their help. I would also like to thank Wang Shu-fang, Chen Wei and Yao Jian for their generous hospitality during my visit to China, as well as the Dept of Botany (NHM) for funding the visit.

TAXONOMY

Bumble bees are a monophyletic group (Williams, 1985*b*, 1995), constituting the tribe Bombini. They may be distinguished from other bees (family Apidae) by the following diagnosis (from Williams, 1991, which includes descriptions of the characters and discussion of homologies):

Bombini have the labrum at least twice as broad as long. The

labrum lacks a longitudinal median ridge, although for the females it has a strong transverse basal depression. The clypeus has a transverse subapical depression and the apico-lateral corners are curved back towards the occiput. A malar area (= malar space) separates the compound eye from the base of the mandible, often by a distance greater than the breadth of the mandible at its base. The hind wings lack a jugal lobe (= anal lobe). The volsella (= lacinia) of the male genitalia is greatly enlarged and is produced apically beyond the gonostylus (= squama).

Bumble bees are large (body length 7–27 mm) robust insects. Their bodies have a dense covering of variously coloured long plumose hairs, although these are few or absent on some parts of the ventral surface of the gaster, on parts of the propodeum, on parts of the anterior face of gastral tergum I, and on parts of the head. The sclerites are usually black, or lighter brown on the distal parts of the limbs, but are never marked with bright yellow, red or metallic (= interference) colours. The wings may be transparent (= hyaline) to strongly darkened (= infuscated), but rarely show strongly metallic reflections.

Female bumble bees have 12 antennal 'segments' (= scape, pedicel and 10 flagellomeres) and six visible gastral terga and sterna (abbreviated to T1–VI, SI–VI). Males have 13 antennal 'segments' (= scape, pedicel and 11 flagellomeres) and seven visible gastral terga and sterna (abbreviated to T1–VII, SI–VII).

Where possible, a divisive, 'top-down' approach to the description of bumble bee diversity has been followed, in the sense of concentrating initially on higher-rank relationships and then distinguishing progressively the species groups, species and then variation within species (as opposed to beginning with described infraspecific taxa and searching 'upwards' for close relatives). At the rank of species, this accepts those putative species or species complexes that are supported by consistent evidence for separate status, and which can be reliably identified throughout their range for the purpose of mapping distributions. This kind of broad over-view at least has the potential to apply consistent criteria across all taxa, even though it is appreciated that not all taxa at the rank of species are necessarily of the same kind (Ackery & Vane-Wright, 1984; de Queiroz & Donoghue, 1988). Specialists will need to modify this list as further information becomes available for particular species groups.

Phylogeny, supra-specific taxa and ordering of species

From available cladistic evidence (Williams, 1991, 1995), use of *Psithyrus* as a genus for the social parasites separate from the remainder of the social bumble bees in *Bombus* can no longer be justified, so a single genus *Bombus* is used for all of the species of bumble bees (see the comments under the subgenus *Psithyrus*).

A system of subgenera has become widely used by

specialists who wish to label assemblages of the more closely similar species. This system is summarised with subgeneric diagnoses and keys by Richards (1968). For a review of supraspecific classifications of bumble bees, see Ito (1985).

The subgeneric system would be more useful if the names were applied only to strictly monophyletic groups. Unfortunately, Richards's (1968) concepts of the bumble bee subgenera do not always agree well with recent estimates of phylogeny, because some of these assemblages now appear to be paraphyletic (e.g. *Mendacibombus*) or even polyphyletic (e.g. *Sibiricobombus* in the sense of Richards, 1968, includes *Obertobombus*, whereas he placed *B. (Sibiricobombus) flaviventris* in *Subterraneobombus*) (Williams, 1991).

Furthermore, the system of subgenera would probably be more useful if it were simplified (e.g. Menke & Carpenter, 1984; and reply by Williams, 1985c). For example, in the New World, both the monophyletic *fraternus*-group of subgenera and the subgenus *Fervidobombus* are endemic, and these are the only two groups represented south of the Panama isthmus. But whereas *Fervidobombus* has been treated nearly consistently as a single, relatively large subgenus (20 species in this list), the *fraternus*-group (18 species in this list) has regularly been split into as many as nine subgenera.

However, no attempt is made in this checklist to revise radically the subgeneric system, because stability will only be served when a revision can be supported by a comprehensive cladistic analysis. This should include not only a broad sample of species, but also a broad range of morphological and molecular characters. Minor modifications from the subgeneric system described by Richards (1968) are detailed in the list after the subgeneric names.

Full synonymy of supraspecific names is included in this checklist, along with details of type species, because these have been revised since Richards (1968). The given generic combination for subgeneric names is shown. Where a genus-group name was published at the rank of genus and subsequently treated at subgeneric rank, the first such action is listed separately. The two-letter abbreviations for subgeneric names are based on those used by Ito (1985).

Species are listed in an order (Table 3) that represents their phylogenetic relationships (after the sequencing convention of Nelson, 1972) as these are currently understood from cladistic studies of the adult morphology of both sexes (Williams, 1995, and many references therein). Within subgenera, this information is still of a very preliminary nature (e.g. Williams, 1991). Many other estimates of relationship exist and would result in different sequences of species names. An alphabetic index is provided as an aid to finding names in this list.

Table 3 List of names for subgenera of the genus *Bombus*, with numbers of species recognised in this checklist. The subgeneric classification is based on Richards (1968), modified to accommodate recent publications (see text; no attempt is made to revise the subgeneric system, because stability will only be served when a revision can be supported by a comprehensive cladistic analysis). Subgenera are listed in an order that represents their phylogenetic relationships (after the sequencing convention of Nelson, 1972) as these are currently understood from cladistic studies of the adult morphology of both sexes (Williams, 1995).

	Subgenus	Number of species
1	<i>Mendacibombus</i>	12
2	<i>Bombias</i>	2
3	<i>Confusibombus</i>	1
4	<i>Mucidobombus</i>	1
5	<i>Eversmannibombus</i>	1
6	<i>Psithyrus</i>	29
7	<i>Laesobombus</i>	1
8	<i>Orientalibombus</i>	3
9	<i>Exilobombus</i>	1
10	<i>Thoracobombus</i>	19
11	<i>Tricornibombus</i>	3
12	<i>Fervidobombus</i>	20
13	<i>Senexibombus</i>	4
14	<i>Diversobombus</i>	4
15	<i>Megabombus</i>	14
16	<i>Rhodobombus</i>	3
17	<i>Kallobombus</i>	1
18	<i>Alpinobombus</i>	5
19	<i>Subterraneobombus</i>	9
20	<i>Alpigenobombus</i>	6
21	<i>Pyrobombus</i>	43
22	<i>Festivobombus</i>	1
23	<i>Rufipedibombus</i>	2
24	<i>Pressibombus</i>	1
25	<i>Bombus s.str.</i>	10
26	<i>Cullumanobombus</i>	2
27	<i>Obertobombus</i>	4
28	<i>Melanobombus</i>	14
29	<i>Sibiricobombus</i>	5
30	<i>Fraternobombus</i>	1
31	<i>Crotchibombus</i>	1
32	<i>Robustobombus</i>	5
33	<i>Separatobombus</i>	2
34	<i>Fuebribombus</i>	2
35	<i>Brachycephalibombus</i>	2
36	<i>Rubictundobombus</i>	1
37	<i>Coccineobombus</i>	2
38	<i>Dasybombus</i>	2

Criteria to discriminate species

It is not possible or appropriate to discuss species concepts in detail in this paper (though the selected references provide some introduction; for recent reviews, see Claridge *et al.*, 1997; Mallet, 1997). However, in order to interpret the checklist, where possible it would be useful to make the species-discriminating criteria explicit. It is equally important to convey the present belief that there is no simple solu-

tion to the problem, and that no single known approach can resolve all of the cases in a uniform and entirely satisfactory manner.

Species concepts (ideas or general notions of the class of objects) and species diagnoses (operational determinations of individual objects) are contentious and probably unresolvable issues. Therefore there is arguably no single 'true' list of species, only more or less valid interpretations from different viewpoints.

Unresolvable conflicts may arise from opposing views of the nature of species. Species have been regarded either as typological classes, with membership to be defined by some shared essence (reviewed by Templeton, 1981), or as individuals, to be discovered (Ghiselin, 1975). There are also conflicting opinions concerning criteria (characteristics or standards by which an object may be judged) for recognising species, based in part on differing emphasis on pattern or process (de Queiroz & Donoghue, 1988).

Species may be considered not to differ from taxa at other ranks (e.g. genera, subspecies) in any qualitative way. There may be quantitative differences in the numbers of character differences that distinguish them in comparison with taxa of lower rank. For example, according to Mallet (1995:294), Darwin (1859) held this view. The problem with quantitative criteria (whether applied to genetic or phenotypic characters) is there is no reason to believe that any choice of threshold in the degree of difference used to recognise taxa at the rank of species is anything other than essentially arbitrary and thus idiosyncratic to particular authors.

In another view, species may be considered to differ qualitatively from taxa at other ranks. It is widely accepted, though often implicitly, that taxa at the rank of species should be recognised so as to mark the boundary between, on the one hand, reticulate relations (for sexually reproducing organisms), and on the other, more consistently divergent genealogical relations. One problem is that this distinction may require predictions as to whether or not currently distinct groups of individuals are likely to show reticulate relationships again in the future.

Interbreeding and the associated genetic recombination is an important part of Dobzhansky's (1937) 'modern synthesis' of Mendelian genetics with Darwin's natural selection theory for evolution. Emphasising interbreeding as a criterion for recognising species characterised what Mayr (1940, 1963) called the 'biological' species concept. These ideas have been modified in the recognition concept of species (Paterson, 1985). One problem with interbreeding or mate recognition as criteria for recognising species is that direct and reliable evidence is rarely available and the results of tests under artificial conditions cannot necessarily be generalised (Splitter, 1982). Another is that the capacity for interbreeding is an

ancestral condition (i.e. not an homology) and so cannot provide support for recognising taxa in the phylogenetic sense (Rosen, 1979).

In practice, all that is usually available to discriminate species as 'different' is evidence from character differences and their patterns of concordance among individuals. The phylogenetic species concept (Cracraft, 1989) is popular because it also embodies the notion that species mark the boundary between different patterns of relationship among individuals and yet it does not rely on inference of interbreeding. The problem is that discovery of phylogenetic species as minimum cladistically-diagnosable (discrete) groups of individuals requires that these groups uniquely share homologies (synapomorphies), which may not always be the case (Ackery & Vane-Wright, 1984; Frost & Kluge, 1994).

Mallet (1995) has argued for minimising the number of assumptions built into species concepts. He suggests that two nominal taxa should be considered conspecific until it can be demonstrated that data for multiple characters distinguish consistent subgroups of individuals with few or no intermediates (the character-cluster concept of species). Although he was arguing against the use of the widely-held biological species concept, he recognised that his prescription differs little from recent common practice. The problem with the cluster concept is how to decide on a threshold for permissible numbers of intermediate individuals between taxa for them still to be considered separate species.

Ultimately, species may be seen as useful conventions to aid in the communication of information gathered about the individuals that are their parts. It may be argued that the most important initial goal is to describe the nature of the variation in each particular case and to avoid presenting only theory-laden (and constrained) interpretations. In this way, basic information on variation will remain available for re-interpretation as theory changes.

For the sake of illustration, four principal classes of problems in geographical variation may be distinguished within the spectrum of kinds of relationships, with the following examples:

Broad co-occurrence of differing individuals

Skorikov (1931) and Reinig (1935) recognised that throughout much of the range of *B. keriensis*, both yellow-banded and cream- or white-banded individuals with indistinguishable morphology co-occur (Fig. 9). From available evidence, it is possible that *B. niveatus* / *vorticatus* may show a similar pattern of yellow/white variation, as may *B. impetuosus* / *potanini*, although with differing degrees of geographical variation in colour-form frequency (see the comments on these species). Consequently, taxa in these pairs are

also treated as conspecific for the present (it is possible that in some cases such colour differences may be controlled by alleles at a single locus, see Owen & Plowright, 1980, on *B. melanopygus*; and Williams, 1991, on *B. asiaticus*; or by small numbers of loci, see Plowright & Owen, 1980, on *B. rufocinctus*). In contrast, although the yellow-banded *B. shaposhnikovii* and the white-banded *B. handlirschianus* also show a broadly-overlapping pattern of distribution, the one white-banded male that I have seen is distinct from the yellow-banded males in the morphology of its genitalia (Williams, 1991).

Broad clinal variation

Many species show broad trends in variation across continents, most obviously in colour pattern (e.g. *B. cingulatus*, Fig. 10; and the *trifasciatus*-group, Fig. 13, which may be combined with locally convergent colour variation, e.g. within the *haemorrhoidalis*-group, *breviceps*-group and *rotundiceps*-group, see Sakagami & Yoshikawa, 1961; Tkalcü, 1968b, 1989). In North America, several pairs of nominal taxa were described originally from individual type-specimens with differing colour patterns from eastern and western regions respectively (e.g. *B. auricomus* / *nevadensis*, *B. fervidus* / *californicus*, *B. pensylvanicus* / *sonorus*, *B. terricola* / *occidentalis*). These taxon pairs have long caused difficulties, for example with Franklin (1913:239) commenting on a list including these taxa and others that are now considered conspecific that 'it must be entirely a matter of personal opinion whether they should be given full species rank or be considered as only subspecies' (although, intriguingly, *B. auricomus* / *nevadensis* were not included in Franklin's list). In at least some of these cases, many individuals with what appears to be a continuum of intermediate colour patterns are now known from broad intervening areas, so that threshold criteria for distinguishing these taxa appear to be essentially arbitrary (e.g. making decisions based on whether a particular tergum has the pubescence entirely yellow, rather than having a few black hairs present). In consequence, taxa in these taxon pairs are treated here as conspecific and maps are compiled for the more clearly recognisable, more inclusive taxa (but see the comments on *B. auricomus* / *nevadensis*).

Narrow hybrid zones

In some cases, otherwise discrete colour forms with closely similar morphology meet in narrow zones (of the order of a few km in breadth), where there may be evidence of intermediate or genetically recombinant individuals. In Europe this is best known for *B. ruderatus* / *argillaceus* (Fig. 11; Scholl, Obrecht & Zimmermann, 1992), and in Asia it has been suggested



Fig. 9 Approximate distribution range (area within the dotted line) and principal colour variation for *B. keriensis* from Reinig (1939: fig. 23). Many more records are available now, but the pattern remains similar, with broad overlap of yellow- and white-banded individuals in Mongolia, Tien Shan, Pamir and western Himalaya. Yellow and cream pubescence is shown on the bees by crosses; red pubescence by vertical hatching.

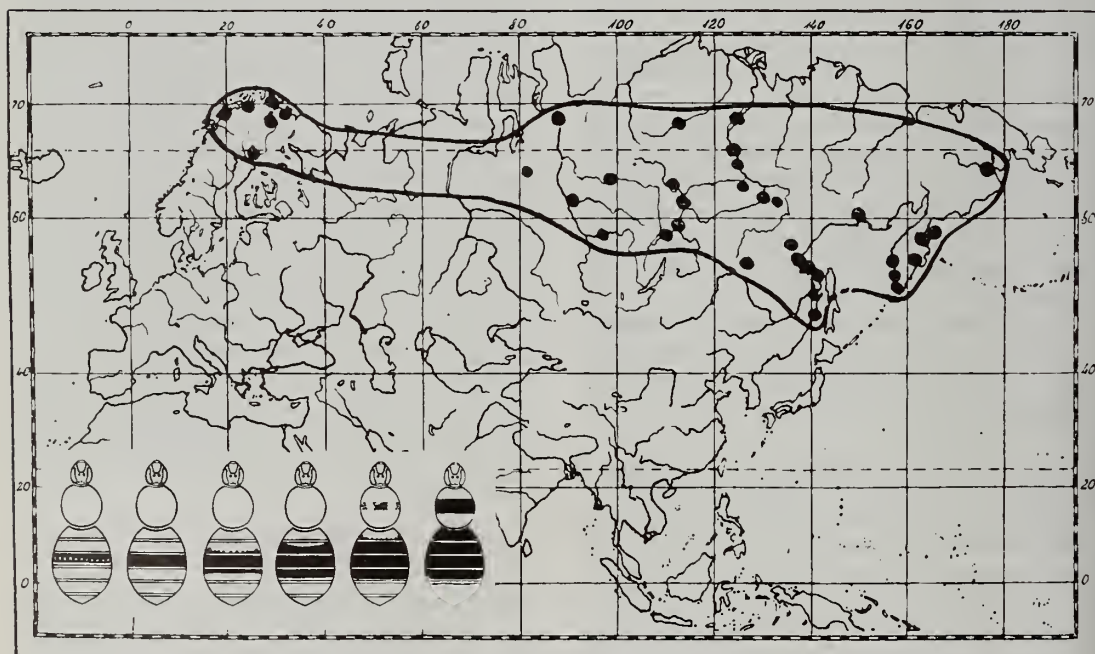


Fig. 10 Distribution records (spots), approximate range (area within the line) and principal colour variation for *B. cingulatus* in the northern Palearctic Region from Reinig (1939: fig. 7). The lightest individuals occur in the east (Kamchatka) and the darkest individuals (with the black thoracic band) occur in the west, with intermediate individuals in intervening areas.



Fig. 11 Distribution records (spots), approximate range (area within the cross-hatching, left, and line, right) and principal colour variation between queens of *B. ruderatus* and *B. argillaceus* in Europe from Reinig (1939: fig. 7). These taxa were regarded as subspecies by Reinig, but have recently been treated as separate species. Although there is evidence of a hybrid zone between some areas of parapatry, the hybrid individuals are very rare (Scholl, Obrecht & Zimmermann, 1992). Yellow pubescence is shown on the bees by crosses.



Fig. 12 Distribution records (spots) and principal colour variation for *B. asiaticus* in Kashmir from Williams (1991: map 48). There is evidence of a hybrid zone between some areas of parapatry, such as some high passes along the divide of the Great Himalaya Range, where there are abundant hybrid individuals. The spot symbols show the locally most abundant colour pattern. Yellow pubescence is shown on the bees by fine stippling; red pubescence by vertical hatching.

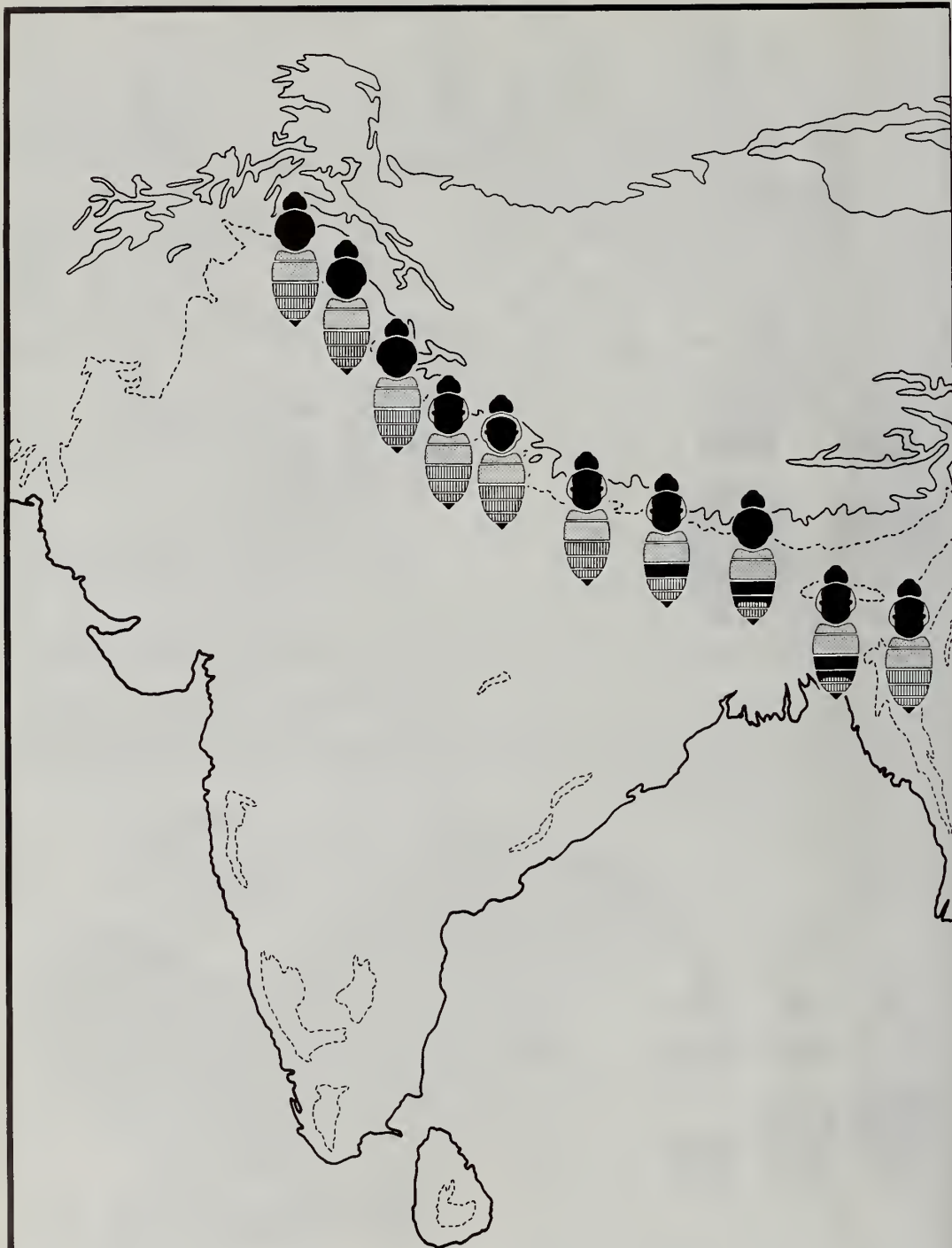
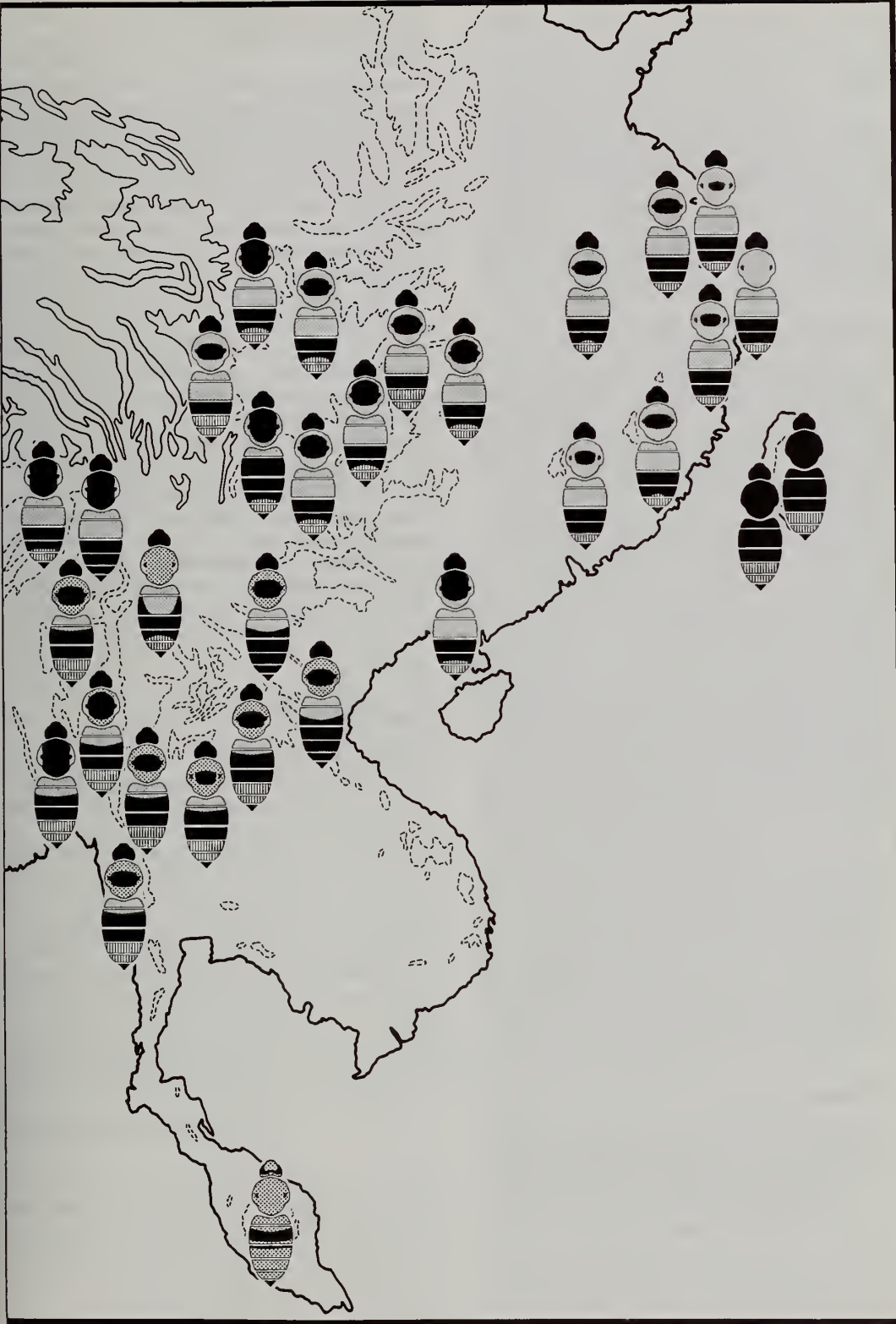


Fig. 13 Distribution records and principal colour variation within the *trifasciatus*-group in Asia (updated from Williams, 1991: fig. 11). The individuals may all be considered parts of a single species, *B. trifasciatus*, depending on which species-defining criterion is accepted. The dashed line shows the 1000 m contour above sea level and the solid line shows the 4000 m contour. Yellow pubescence is shown on the bees by fine stippling, orange pubescence by coarse stippling, red pubescence by vertical hatching.



for *B. asiaticus* / *longiceps* (Fig. 12; Williams, 1991). Other possible examples include *B. lapponicus* / *monticola* in Europe and *B. pyrosoma* / *friseanus* / *miniatus* in China. In the case of *B. asiaticus* / *longiceps*, I have treated them as conspecific, because intermediate individuals greatly outnumber 'typical' individuals at some localities. For the other cases, I have followed earlier treatments of these taxa as separate species, because intermediate individuals are rare or not well known (although this may be a consequence of poor sampling in some inaccessible areas).

Disjunct peripheral populations

Some peripheral populations on offshore islands or habitat islands (e.g. mountains) show some divergence in colour pattern with little morphological divergence. European examples include *B. terrestris* / *canariensis* and *B. hortorum* / *reinigiellus*. Asian examples include *B. schrencki* / *honshuensis*, *B. trifasciatus* / *maxwelli* (Fig. 13, Peninsular Malaysia), *B. trifasciatus* / *wilemani* (Fig. 13, Taiwan), *B. breviceps* / *angustus*, *B. parthenius* / *sonani*, *B. flavescens* / *rufoflavus* and *B. flavescens* / *baguionensis*. For the application of the biological species concept, in these cases there is no 'natural' meeting of individuals between the taxon pairs and so no admissible evidence on interbreeding (Splitter, 1982). For the application of Mallet's (1995) cluster concept, quantitative analysis of patterns of variation is urgently needed. Where this information is absent, I agree with his prescription of treating taxa in these taxon pairs as provisionally conspecific. *Bombus honshuensis* and *B. schrencki* are mapped separately here because, from published accounts and a small sample of material examined, their colour differences appear to coincide with stronger and more consistent morphological distinctions.

It is hoped that further information may help to clarify these cases. In the interests of pluralism, I aim to report not only a preferred interpretation in the comments on each species, but also at least the more widely-held alternative interpretations.

Sub-specific taxa

For this checklist the interest is primarily in problems of recognition and nomenclature for taxa at the rank of species. Subspecific names refer to parts of species, and so for present purposes these can be treated as synonyms of specific names (e.g. Schwarz *et al.*, 1996). This is not to say that subspecific taxa should not be recognised if they are considered useful, and of course other biologists may add subspecies to this list (cf. Rasmont *et al.*, 1995).

NOMENCLATURE

Nomenclature should be seen as the servant of biology: its purpose is to provide labels that enable biologists to communicate information about organisms with minimal confusion concerning the organisms to which they refer. Accounts of the history of nomenclature for many groups of organisms (e.g. on British bumble bees: Alford, 1975; Prŷs-Jones & Corbet, 1987:82) show that this is not a trivial matter and that rules are necessary.

Treatment of names follows the *International Code of Zoological Nomenclature* (International Commission on Zoological Nomenclature [ICZN], 1985). The Principle of Priority is generally adhered to, although regard is given to the stated purpose of priority (ICZN, 1985: Article 23b): namely that it should be used to promote stability and is not intended to be used to upset a long-accepted name in its accustomed meaning (Article 79c) through the introduction of an unused name that is its senior synonym. Similar action is also suggested where cases of homonymy affect current usage, although this action cannot be taken when it is felt desirable to maintain availability of a senior homonym. My suggestions for applications to ICZN for conservation of names in current use are indicated by stars (★).

Typographical conventions

<i>Bombus b-us</i>	valid name in the species group,
<i>c-us</i>	available name in the species group, including synonyms of a valid species name,
<i>?d-us</i>	available name in the species group, a provisional synonym of a valid species name,
<i>[e-us]</i>	unavailable name, informally associated with a valid species name,
<i>f-us</i> examined	type material for species-group name
●	<i>f-us</i> examined (in whole or in part),
○	comments on status of species,
★	comments on application of names,
<i>?Bombus g-us</i>	suggestion for application to ICZN.
	valid name in the species group, for a taxon that is recognised provisionally as a separate species from <i>B. b-us</i> .

A question mark (?) before a valid name shows that, while it refers to a taxon that is considered likely to be a separate species, it may be conspecific with the preceding taxon in the list (i.e. while *Bombus g-us* may be conspecific with *Bombus b-us*, *Bombus d-us* is much more likely to be conspecific with *Bombus b-us*).

Names in the more detailed references are followed by names of authors, date of first publication (within the meaning of ICZN, 1985), and page reference. Wherever possible, the true first date of publication is given in preference to any purported date of publication when these differ. If a name were published originally in a different generic combination, then the original genus is shown in brackets. If the name had been published originally with a different termination, or with capital initial letters, diacritic marks etc., then the original form is shown without the mandatory changes (with the exception that small capital letters are reduced to lower case).

Selection of synonyms

This checklist is based on a much longer catalogue of over 2800 names. As a checklist, it is not required to include the full list of synonyms, so synonyms are selected for this list primarily where they help to clarify the identity and scope of the species (including the subspecies included by some authors), particularly with reference to those names in most common use in the literature of the last 25 years. Misidentifications are not included with the lists of synonyms and are discussed only when necessary to clarify the application of problematic names.

Applications to ICZN

Flexibility in interpretation of the status of taxa is possible where the evidence to distinguish among interpretations is absent, inconclusive, or may permit different interpretations under different species concepts. Otherwise flexibility in the application of names depends on whether systematists are eager to apply to the International Commission on Zoological Nomenclature to use its Plenary Power in order to conserve a preferred usage of names (e.g. Løken *et al.*, 1994; ICZN, 1996).

I propose that this could be achieved in a single application to include all names for which action is currently known to be required (*atratus*, *balteatus*, *distinguendus*, *flavifrons*, *humilis*, *hyperboreus*, *mesomelas*, *mixtus*, *norvegicus*, *polaris*, *pyrenaicus*, *soroeensis* and *variabilis*). Comments on this proposal would be welcomed.

DISTRIBUTION MAPS

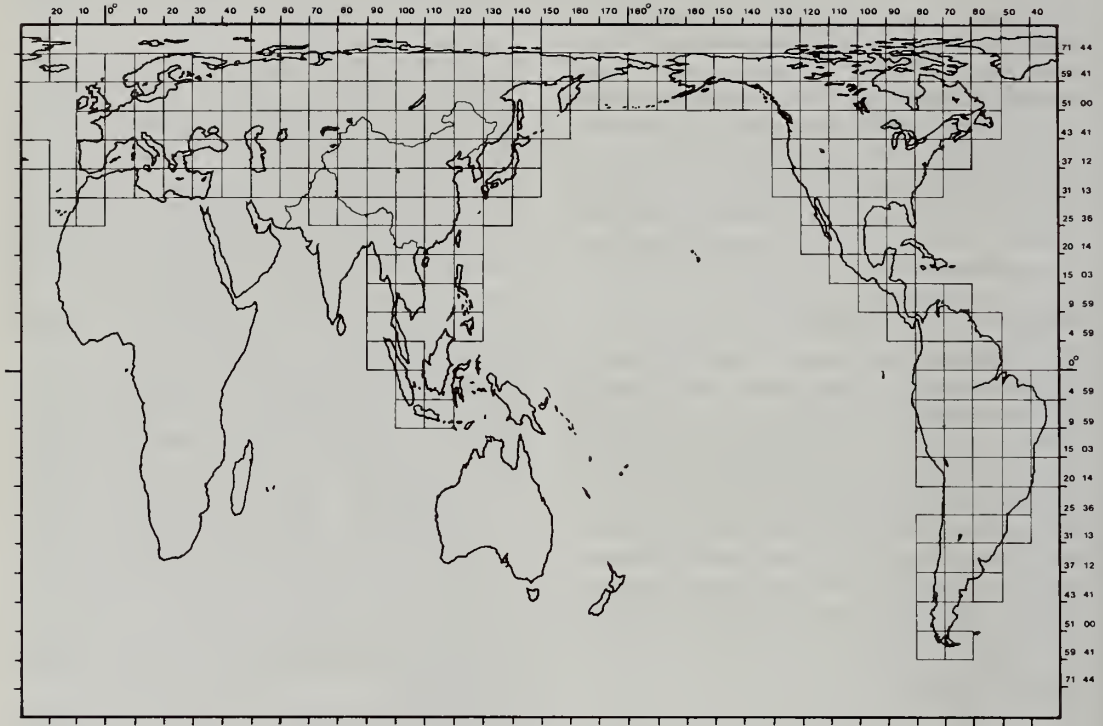
This checklist was compiled in conjunction with distribution data in support of biogeographic studies.

Maps of world-wide distribution at a coarse grain size were designed for use in comparisons of regional bumble bee faunas (e.g. Williams, 1989, 1991, 1993, 1995, 1996a, b; Williams & Seddon, 1993; Williams & Humphries, 1996).

Aside from any difficulties in identifying species or localities, comparisons among faunas are complicated by two principal factors: first, by differences in sampling effort (as illustrated by 'species-accumulation curves', e.g. Colwell & Coddington, 1994); and second, by differences in the extent of sampling areas ('species-area effects', e.g. Connor & McCoy, 1979). Fortunately for the first problem, the attractiveness of bumble bees to collectors has ensured that they have been relatively intensively sampled, so that most faunas are relatively well known. But in order to reduce this problem further, rather than extrapolate local richness and lose information on individual species, the expected distributions of some species are interpolated on the basis of knowledge of their habitat associations (see the legend to Fig. 14). To reduce the second problem of species-area effects, equal-area grid cells were established using a cylindrical, equal-area projection of the world, marked at intervals of 10° of longitude and calculated intervals of latitude (Fig. 14). However, this does not ensure equal land areas among grid cells, or equal areas of habitat suitable for bumble bees.

Because the intention is to study biogeographic patterns, maps are required to show all historical records, including data from areas where species may now be extinct. On the other hand, data exclude fossil taxa (reviewed by Zeuner & Manning, 1976) and documented introductions (e.g. Oliff, 1895; Frison, 1925b; Gurr, 1957; Prŷs-Jones *et al.*, 1981; Arretz & Macfarlane, 1982; Cardale, 1993).

The maps for every species are not included with this checklist because many data are still being collected, although for each subgenus a preliminary map of species richness is included as a general guide (or for monotypic subgenera, a map of records for the single species is included). The numerical values for the grey-scale classes differ between maps and are not shown. This is because I have adopted an alternative approach of using equal frequency classes, which have the advantage that each grey-scale class remains consistent in its relative richness among all maps (e.g. dark grey always shows the richest one fifth of occupied cells excluding the maximum etc.). The sources of the distribution data have not been included because this will be included in a later atlas.



Key to map symbols:

Maps for single species

- specimens examined,
- precise literature records (e.g. 'Dungeness TR01, UK'),
- vague locality data (e.g. 'Florida'),
- interpolations of expected distribution (following common practice for range-filling maps; the rules adopted here are to fill cells between occupied cells when filled cells are known to have had a high proportion of suitable habitat within recorded history; these records amount to < 10% of all gridcell records at this scale, Williams, 1993).

Maps for multiple species



maximum species counts are shown in black, otherwise counts are divided into five grey-scale classes of approximately equal size by numbers of grid cells.

Fig. 14 Map of the world (excluding Antarctica) using a cylindrical equal-area projection that is orthomorphic (minimum shape distortion) at 46° North and South (where bumble bee records are particularly plentiful). Intervals of 10° longitude (top of map) are used to calculate intervals of latitude (right of map) that provide equal-area grid cells of c. 611,000 km². The portion of the grid shown covers the known, native distribution of bumble bees. Map symbols are shown above for (a) plotting individual species, for which different spots distinguish different data categories (Map 3); or (b) for plotting coincidence maps for multiple species, using a grey scale for variation in species richness (Map 1).

LIST OF SPECIES



(plot of total species richness with grey scale, for explanation see Fig. 14)

Genus **BOMBUS** Latreille in the broad sense

[*Bremus* Jurine], 1801:164, type-species *Apis terrestris* Linnaeus (= *Bombus terrestris* (Linnaeus)) by subsequent designation of Morice & Durrant, 1915:429, suppressed by ICZN, 1939]

Bombus Latreille, 1802a:437, type-species *Apis terrestris* Linnaeus (cited as *Apis terrestris* F.) (= *Bombus terrestris* (Linnaeus)) by monotypy

Bombus Latreille, 1802b:385, type-species *Apis terrestris* Linnaeus (= *Bombus terrestris* (Linnaeus)) by monotypy, redescribed

[*Bremus* Panzer, 1805:pl. 19–21, type-species *Apis agrorum* Fabricius (= *Bombus pascuorum* (Scopoli)) by subsequent designation of Sandhouse, 1943:532, suppressed by ICZN, 1954]

[*Bombellus* IIE, 1931:248, incorrect subsequent spelling]

Subgenus **MENDACIBOMBUS** Skorikov

Mendacibombus Skorikov, 1914a:125, type-species *Bombus mendax* Gerstaecker by subsequent designation of Sandhouse, 1943:572

Bombus (*Mendacibombus*) Krüger, 1917:62

COMMENT. The species of *Mendacibombus* appear to be paraphyletic with respect to the rest of the

bumble bees and in consequence are not a 'natural' group (Williams, 1991, 1995).

Bombus* (Md.) *avinoviellus (Skorikov)

avinoviellus (Skorikov, 1914a:126 [*Mendacibombus*]) examined

callophenax Cockerell, 1917:122, examined

Bombus* (Md.) *mendax Gerstaecker

mendax Gerstaecker, 1869:323, examined

latofasciatus Vogt, 1909:50, not of Vogt, 1909:42 (= *B. lucorum* (Linnaeus))

pyrenes (Tkalčú, 1975:173 [*Mendacibombus*]) replacement name for *latofasciatus* Vogt, 1909:50

Bombus* (Md.) *makarjini Skorikov

makarjini Skorikov, 1910a:329, examined

Bombus* (Md.) *superbus (Tkalčú)

superbus (Tkalčú, 1968a:22 [*Mendacibombus*]) examined

Bombus* (Md.) *himalayanus (Skorikov)

?*varius* (Skorikov, 1914a:125 [*Mendacibombus*]) examined, not of Lepeletier, 1832:381 (= *B. campestris* (Panzer))

himalayanus (Skorikov, 1914a:127 [*Mendacibombus*]) examined

Bombus* (Md.) *marussinus Skorikov

marussinus Skorikov, 1910a:330, examined

afghanus Reinig, 1940:230, examined

Bombus* (Md.) *turkestanicus Skorikov

turkestanicus Skorikov, 1910a:329, examined

Bombus* (Md.) *defector Skorikov

defector Skorikov, 1910a:330

?*altaicus* Skorikov, 1910a:329, not of Eversmann, 1846:436 (= *B. melanurus* Lepeletier)

?*margreiteri* Vogt, in Skorikov, 1910a:330, examined

● TAXONOMIC STATUS. Skorikov's (1910a) descriptions of varieties of *B. mendax* are all of females. Many of these nominal taxa have subsequently been treated as separate species (e.g. Skorikov, 1931; Rasmont, 1988).

However, I have examined type material or other material identified by Skorikov for all of these taxa and find some of them to be morphologically closely similar. The females of *defector*, *altaicus* and *margreiteri* differ from one another principally in

colour, and the only males I have seen associated with them (collections in London, Petersburg, Beijing) have very similar genitalia (which are distinct from *B. mendax*).

Until more evidence to the contrary is available from critical studies of patterns of variation, I shall continue to treat *B. defector*, *B. altaicus* and *B. margreiteri* as parts of a single variable species, *B. defector* (Williams, 1985a, 1991).

○ NOMENCLATURE. Williams (1991) regarded *B. defector*, *B. altaicus* and *B. margreiteri* as likely to be conspecific and following the Principle of First Reviser (ICZN, 1985: Article 24) chose *B. defector* as the name for the species.

***Bombus (Md.) handlirschianus* Vogt**

Handlirschianus Vogt, 1909:49

***Bombus (Md.) shaposhnikovi* Skorikov**

shaposhnikovi Skorikov, 1910a:329

***Bombus (Md.) waltoni* Cockerell**

chinensis Skorikov, 1910a:330, examined, not of Morawitz, 1890:352 (= *B. chinensis* (Morawitz))
waltoni Cockerell, 1910b:239, examined

***Bombus (Md.) convexus* Wang**

lugubris Morawitz, 1880:339, examined, not of Kriechbaumer, 1870:159 (= *B. maxillosus* Klug)
convexus Wang, 1979:190, examined



Subgenus BOMBIA Robertson

Bombias Robertson, 1903:176, type-species *Bombias auricomus* Robertson (?= *Bombus nevadensis* Cresson) by original designation

Bombus (*Bombias*) Franklin, 1913:138

Nevadensibombus Skorikov, 1922a:149, type-species *Bombus nevadensis* Cresson by subsequent designation of Frison, 1927:64

Bremus (*Boopobombus*) Frison, 1927:59 (proposed as a

section name but stated by Frison to include those forms considered by Franklin, 1913, to belong to the subgenus *Bombias* Robertson), type-species *Bombias auricomus* Robertson (= *Bombus auricomus* (Robertson)) by subsequent designation of Williams, 1995:339.

***Bombus (Bi.) nevadensis* Cresson**

nevadensis Cresson, 1874:102

COMMENT. A single queen of *B. nevadensis* has been reported from Hidalgo, Mexico, by Milliron (1971) and Hurd (1979), although the species is not listed for Mexico by Labougle (1990).

?*Bombus (Bi.) auricomus* (Robertson)

auricomus (Robertson, 1903:176 [*Bombias*])

● TAXONOMIC STATUS. *B. nevadensis* and *B. auricomus* have been regarded both as conspecific (e.g. LaBerge & Webb, 1962; Milliron, 1971; Thorp *et al.*, 1983; Laverty & Harder, 1988) and as separate species (e.g. Franklin, 1913; Rasmont, 1988; Scholl, Thorp, Owen & Obrecht, 1992; Poole, 1996).

B. nevadensis from western North America was not mentioned in the original description of *B. auricomus* (lectotype worker from Illinois by designation of Milliron, 1971:78), although the latter was described using characters of morphology and of colour pattern. The two taxa have generally been distinguished on the basis of the extent of the black pubescence on the dorsum of the female thorax and laterally on the male gastral terga (e.g. Franklin, 1913).

The only study to investigate variation in characters used to distinguish the two taxa at a fine spatial scale in their area of overlap was by LaBerge & Webb (1962). They reported (p. 26) that 'Throughout the broad middle half of Nebraska *nevadensis* seems to be rather rare and most specimens, although referable to subspecies *auricomus* show some indication of intergrading with the typical subspecies [*nevadensis*] in the west. . . . Many specimens from Nebraska in the range of the typical subspecies [*nevadensis*] show some tendency toward the darker coloration of subspecies *auricomus*.' They concluded that these variable bees are all parts of the same species.

Recently, Scholl *et al.* (1992) distinguished two groups of individuals on the basis of differing mobility morphs of five enzymes. The individuals in one enzyme group were all extensively dark-banded, and Scholl *et al.* associated these with the name *B. auricomus*. However, individuals in the other enzyme group, which Scholl *et al.* associated with the name *B. nevadensis*, apparently included not only the contrasting, extensively pale individuals (*B. nevadensis*), but also a few of the extensively dark-banded individuals (*B. auricomus*) similar to those in the first group (8/49

individuals had gastral tergum I almost completely black; 3/49 individuals had the scutellum predominantly black). Thus the enzyme evidence does identify two groups of individuals, but (1) these do not appear to correspond precisely to the two traditional colour groups; (2) some of the key areas likely to support intermediate or recombinant individuals still need to be sampled for enzyme variation (e.g. in the Dakotas, L. Day *in litt.*); and (3) inheritance of enzyme and colour states needs to be better understood, including the unusual enzyme morphs of the heterozygous bees (detected in 20/141 queens). They concluded that these bees represent two species.

A. Scholl (*in litt.*) reports a further intriguing morphometric study. A random subsample of 20 queens from the enzyme study was scored for 15 characters and analysed by linear discriminant analysis. This method seeks a combination of characters that best discriminates any two *a priori* sets, in this case using three measurements of parts of the radial cell, eye and antenna. However, although this approach may be useful for discriminating previously recognised taxa, it does not provide evidence that they are necessarily separate species (it could also be used to discriminate morphological subsets within a single, variable population, e.g. among breeds of domestic dogs).

From an examination of 41 females, so far I have found only one subtle morphological character to distinguish eastern, banded bees (*B. auricomus*), on the one hand, from western unbanded (*B. nevadensis*) and banded (e.g. Vancouver Island) bees, on the other. This concerns the anterior part of a band of large punctures along the inner eye margin, dorsally opposite the ocelli, just before these punctures meet a more anterior, very dense patch of small punctures. The western bees have areas between the large punctures conspicuously shining, with few fine punctures and lacking microsculpture. In contrast, the eastern bees have these areas appearing rather dull, often with more of the fine punctures, and more particularly with a very fine, wrinkled or reticulate microsculpture. A similar difference may be present in the males, posteriorly to the ocelli, though the sample sizes available to me are too small for much confidence.

I regard the conflicting evidence available at present as not entirely conclusive as to whether these bees are parts of the same population or two separate species. As far as is known, both the variations of the colour pattern and of the enzyme mobilities are inherited and genetically determined, but details of patterns of inheritance and of the spatial aspects of any association between these characters are unknown. In view of the multiple enzymes differences found and of the apparent association between the enzyme groups and the morphological character states, I shall follow the treatment of these taxa as two separate species until more evidence is available.



(plot of records for a single species, for explanation and key see Fig. 14)

Subgenus *CONFUSIBOMBUS* Ball

Bombus (*Confusibombus*) Ball, 1914:78, type-species

Bombus confusus Schenck by monotypy

Bombus (*Sulcobombus*) Krüger, 1917:65, type-species

Bombus confusus Schenck by subsequent designation of Sandhouse, 1943:602

Confusobombus Skorikov, 1922a:156, type-species

Bombus confusus Schenck by subsequent designation of Richards, 1968:214

Bombus (Cf.) *confusus* Schenck

confusus Schenck, 1859:135

paradoxus Dalla Torre, 1882:18

festivus Hoffer, 1882:80, not of Smith, 1861:152 (= *B. festivus* Smith)

● TAXONOMIC STATUS. *B. confusus* and *B. paradoxus* differ in the colour pattern of the pubescence (e.g. Reinig, 1939: fig. 19). Rasmont (1988) reports that in north western Europe, the yellow-banded and white-tailed *B. paradoxus* occurs only as rare individuals within the population of predominantly unbanded and red-tailed *B. confusus*. In contrast, all of the individuals that I have seen from the disjunct population in Central Asia have the yellow-banded and white-tailed *B. paradoxus* colour pattern.



Subgenus *MUCIDOBOMBUS* Krüger

Mucidobombus Krüger, 1920:350, type-species *Bombus*

mucidus Gerstaecker by monotypy

Bombus (*Mucidobombus*) Pittioni, 1937:97

Bombus* (Mc.) *mucidus* Gerstaeckermucidus* Gerstaecker, 1869:324*atratus* Friese, 1911:572, examined**Subgenus *EVERSMANNIBOMBUS* Skorikov***Agribombus* (*Eversmannibombus*) Skorikov, 1938a:145, type-species *Mucidobombus eversmanniellus* (= *Bombus persicus* Radoszkowski) by monotypy*Bombus* (*Eversmannibombus*) Richards, 1968:214***Bombus* (Ev.) *persicus* Radoszkowski***calidus* Eversmann, 1852:133, examined, not of Erichson in Middendorff, 1851:65 (= *B. hypnorum* (Linnaeus))*persicus* Radoszkowski, 1881:v, examined*Persicus* Radoszkowski, 1883:214, redescribed*eversmanni* Friese, 1911:572, not of Skorikov, 1910c:581 (= *B. modestus* Eversmann), replacement name for*calidus* Eversmann, 1852:133*eversmanniellus* (Skorikov, 1922a:149 [*Mucidobombus*]) replacement name for *eversmanni* Friese, 1911:572**Subgenus *PSITHYRUS* Lepeletier***Psithyrus* Lepeletier, 1832:373, type-species *Apis rupestris* Fabricius (= *Bombus rupestris* (Fabricius)) by subsequent designation of Sandhouse, 1943:572*Apathus* Newman, 1835:404, replacement name for *Psithyrus* Lepeletier, incorrectly stated to be a junior homonym of *Psithyros* Hübner, [1819]:132 (= *Macroglossum* Scopoli, 1777:414)? *Psithyrus* (*Labiropsithyrus*) Frison, 1927:69, type-species *Bombus laboriosus* Fabricius (= *Emphoropsis laboriosus* (Fabricius) in the sense of Frison (= *Bombus citrinus* (Smith)), a misidentification, see Milliron, 1960:99, requiring designation by ICZN) by original fixation ☼*Psithyrus* (*Ashtonipsithyrus*) Frison, 1927:69, type-species *Apathus ashtoni* Cresson (= *Bombus ashtoni* (Cresson)) by original designation*Psithyrus* (*Fernaldaepsithyrus*) Frison, 1927:70, type-species *Psithyrus fernaldae* Franklin (= *Bombus fernaldae* (Franklin)) by original designation*Psithyrus* (*Eopsithyrus*) Popov, 1931:134, type-species *Apathus tibetanus* Morawitz (= *Bombus tibetanus* (Morawitz)) by original designation*Psithyrus* (*Metapsithyrus*) Popov, 1931:135, type-species *Apis campestris* Panzer (= *Bombus campestris* (Panzer)) by original designation*Psithyrus* (*Allopsithyrus*) Popov, 1931:136, type-species *Apis barbutella* Kirby (= *Bombus barbutellus* (Kirby)) by original designation*Psithyrus* (*Ceratopsithyrus*) Pittioni, 1949:270, type-species *Psithyrus klapperichi* Pittioni (= *Bombus cornutus* (Frison)) by original designation*Psithyrus* (*Citrinopsithyrus*) Thorp in Thorp *et al.*, 1983:50, type-species *Apathus citrinus* Smith (= *Bombus citrinus* (Smith)) by original designation*Bombus* (*Psithyrus*) Williams, 1991:44[*Psithyrus* (*Fernaldepsithyrus*) Amiet, 1996:86, incorrect subsequent spelling]

● **TAXONOMIC STATUS.** It has long been considered useful to regard *Psithyrus* as a separate genus in recognition of the distinctive behaviour of the species, as social parasites in colonies of the remaining Bombini, and in recognition of their distinctive morphology. However, most recent studies have shown (if phenograms are interpreted along with cladograms as phylogenetic estimates) that, although *Psithyrus* is itself very likely to be monophyletic, the remaining bumble bees are not (Plowright & Stephen, 1973; Obrecht & Scholl, 1981; Ito, 1985; Williams, 1985b, 1991, 1995; Pamilo *et al.*, 1987).

I have previously attempted to retain the use of the names *Psithyrus* and *Bombus* for monophyletic genera by recognising a third genus, *Mendacibombus* (Williams, 1985b). However, further study of all of the species of *Mendacibombus* (Williams, 1991, 1995) showed that it is likely to be paraphyletic with respect to all other bumble bees, with the consequence that as many as another nine genera (mostly for single species) might be required to maintain monophyly alongside a genus *Psithyrus*. In the face of this evidence, a pragmatic solution was recommended, recognising a single genus *Bombus* for all bumble bees, to include *Psithyrus* as a subgenus. This is a return to an emphasis of the more widely shared characters and the more distant affinities for the generic concept, encouraged by the opinion of Michener (1990) that bumble bees are 'morphologically mo-

notonous' in comparison with variation among species within closely related groups such as Euglossini (orchid bees) and Meliponini (stingless bees). One advantage of a single genus for all bumble bees is that it recognises a group for which evidence of monophyly is particularly strong, so that nomenclature is most likely to remain stable in the future. Use of a single genus *Bombus* for all bumble bees (Williams, 1991) has now been accepted by most recent authors (e.g. Rasmont & Adamski, 1995; Rasmont *et al.*, 1995; Schwarz *et al.*, 1996).

The subgenera within the former genus *Psithyrus* have often been considered less distinct from one another than have the other subgenera of *Bombus* (Pittioni, 1939a; Ito, 1985; Williams, 1985b; Michener, 1990) and therefore may be treated as synonyms of *Psithyrus* (Milliron, 1961; Williams, 1991, 1995). In an alternative treatment, Rasmont *et al.* (1995) include the former subgenera of the former genus *Psithyrus* as separate subgenera within the genus *Bombus*.

○ NOMENCLATURE. The names of six species of the subgenus *Psithyrus* from Kashmir were explicitly stated to be new combinations with the genus *Bombus* by Williams (1991). Rasmont *et al.* (1995) have since listed the other European species in this combination. No formal statements of new combination are made here for the remaining species of the subgenus *Psithyrus* because a principle of implied combinations (Poole, 1996) is followed after the change in status of *Psithyrus* from genus to a subgenus of *Bombus*.

✱ APPLICATION TO ICZN. Because the type species of *Laboriopsithyrus* was misidentified (discussed by Milliron, 1960:99), ICZN is required to designate as type species whichever species will best serve nomenclatural stability (ICZN, 1985: Art. 70b). It is suggested that, in the interests of stability (ICZN, 1985: Article 23b), an application be made to ICZN to use its Plenary Power to select the species actually involved (*Bombus laboriosus* in the sense of Frison, = *Bombus citrinus* (Smith)), which was wrongly named in the type fixation (ICZN, 1985: Art. 70b(i)).

COMMENT. The highest richness of species of the subgenus *Psithyrus* occurs in the Old World (there are no species known from south of Panama), although the earliest-diverging species appear to be North American (unpublished). This is the opposite pattern to that shown by species of the largest subgenus, *Pyrobombus* (see the comments on the subgenus *Pyrobombus*).

All species of the subgenus *Psithyrus* are believed to be obligate social parasites in colonies of other *Bombus* species (reviewed by Alford, 1975; Fisher, 1987). There is variation in the degree of host specificity. See also the comments on *B. inexpectatus* and *B. hyperboreus*.

Bombus (Ps.) *insularis* (Smith)

interruptus Greene, 1858:11, not of Lepeletier, 1832:381 (= *B. rupestris* (Fabricius))

insularis (Smith, 1861:155 [*Apathus*]) examined
consultus (Franklin, 1913:459 [*Psithyrus*])

?*bicolor* (Franklin, 1913:460 [*Psithyrus*]) not of Höppner, 1897:33 (= *B. soroensis* (Fabricius)) (provisional synonym)

crawfordi (Franklin, 1913:464 [*Psithyrus*])

● TAXONOMIC STATUS. According to D. Yanega (*in litt.*), who has examined the type material, *B. bicolor* Franklin is conspecific with *B. interruptus*.

Bombus (Ps.) *citrinus* (Smith)

citrinus (Smith, 1854:385 [*Apathus*]) examined
contiguus (Cresson, 1863:112 [*Apathus*])

Bombus (Ps.) *variabilis* (Cresson)✱

intrudens (Smith, 1861:154 [*Apathus*]) examined

variabilis (Cresson, 1872:284 [*Apathus*]) new synonym

?*guatemalensis* (Cockerell, 1912:21 [*Psithyrus*]) (provisional synonym)

?*sololensis* (Franklin, 1915:173 [*Psithyrus*]) (provisional synonym)

?*mysticus* (Frison, 1925a:138 [*Psithyrus*]) (provisional synonym)

● TAXONOMIC STATUS. Specimens in the NHM collection from Mexico and Guatemala labelled '*intrudens*' and '*sololensis*' appear to me to be closely similar to *B. variabilis*. Frison (1925a) believed that *B. sololensis* is a colour form of *B. guatemalensis*. Nevertheless, he proceeded to distinguish *B. mysticus* as a separate species on the basis of colour pattern alone. I am unaware of any reason (other than minor differences in colour pattern) why *B. variabilis*, *B. intrudens*, *B. sololensis*, or *B. guatemalensis* and *B. mysticus* (judging from the published descriptions at least), should not be considered conspecific.

○ NOMENCLATURE. A female in the NHM collection has three labels '*Apathus / intrudens / Smith*', '58.135 MEX. / (Oajaca.)', 'Holo- / type' and I am unaware of any problems with this designation. If this is correct and the type is conspecific with *B. variabilis*, then *B. intrudens* is the oldest available name for this species. D. Yanega (*in litt.*) agrees with this interpretation.

✱ APPLICATION TO ICZN. Although *B. intrudens* is the oldest available name for the present interpretation of this species, the name *B. variabilis* has been in common use for the species since 1947 (e.g. Stevens, 1948; Chandler, 1950; LaBerge & Webb, 1962; Mitchell, 1962; Medler & Carney, 1963; Hobbs, 1966; Plowright & Stephen, 1973; Hurd, 1979; Husband *et al.*, 1980; Michener, 1990; Poole, 1996). I know of no publications using the name *B. intrudens* since 1947. It

is suggested that, in the interests of stability (ICZN, 1985: Article 23b), an application be made to ICZN to use its Plenary Power to suppress the unused senior synonym (ICZN, 1985: Article 79) (see the comments on *B. muscorum*). However, the consequence of this action would be that *B. intrudens* would no longer be available for a species or for a subspecies of *B. variabilis* (Cresson).

***Bombus (Ps.) suckleyi* Greene**

Suckleyi Greene, 1860:169

***Bombus (Ps.) vestalis* (Geoffroy)**

vestalis (Geoffroy in Fourcroy, 1785[see Hagen 1862:246]:450 [*Apis*])

***Bombus (Ps.) perezii* (Schulthess-Rechberg)**

perezii (Schulthess-Rechberg, 1886:275 [*Psithyrus*])

***Bombus (Ps.) ashtoni* (Cresson)**

Ashtoni (Cresson, 1864:42 [*Apathus*])

***Bombus (Ps.) bohemicus* Seidl**

nemorumi (Fabricius, 1775:380 [*Apis*]) examined, not of Scopoli, 1763:307 (= *B. subterraneus* (Linnaeus)), not of Fabricius, 1775:382 (= *B. distinguendus* Morawitz)

bohemicus Seidl, 1837:73

?chinganicus (Reinig, 1936:8 [*Psithyrus*]) (provisional synonym)

hedini (Bischoff, 1936:26 [*Psithyrus*]) not of Bischoff, 1936:15 (= *B. hedini* Bischoff)

● TAXONOMIC STATUS. I am unaware of any reason (other than the small body size of the holotype female and three paratype females of *B. chinganicus*) why *B. bohemicus* and *B. chinganicus* should not be considered conspecific. Consistent with this, body sizes do appear to vary considerably within British species of the subgenus *Psithyrus*, including *B. bohemicus*.

***Bombus (Ps.) coreanus* (Yasumatsu)**

coreanus (Yasumatsu, 1934:399 [*Psithyrus*])

***Bombus (Ps.) barbutellus* (Kirby)**

Barbutella (Kirby, 1802:343 [*Apis*]) examined

?richardsi (Popov, 1931:150, 190 [*Psithyrus*]) not of Frison, 1930:6 (= *B. rufipes* Lepeletier)

?licenti (Maa, 1948:34 [*Psithyrus*]) examined

○ NOMENCLATURE. Løken (1984) interpreted *B. saltuum* (Panzer, 1801) as conspecific with *B. barbutellus*. Consequently, *B. saltuum* would appear to be the oldest available name for this species. However, Løken made no further comment on this and used the name *Psithyrus barbutellus* (= *B. barbutellus*), possibly because she remained unsure of the identity of *B. saltuum*. In contrast, Warncke (1986) interpreted

B. saltuum as conspecific with *B. subterraneus*. See the comments on *B. subterraneus*.

***?Bombus (Ps.) maxillosus* Klug**

maxillosus Klug in Germar, 1817:269

lugubris (Kriechbaumer, 1870:159 [*Psithyrus*])

unicolor (Kriechbaumer, 1870:159 [*Psithyrus*])

mixta (Kriechbaumer, 1870:160 [*Psithyrus*])

šusterai (May, 1944:267 [*Psithyrus*]) not infrasubspecific after Tkalcü, 1977:224

● TAXONOMIC STATUS. As Rasmont (1988) notes, *B. maxillosus* is closely similar to *B. barbutellus* in morphology and habitat, so that specimens cannot always be distinguished reliably. Consequently these nominal taxa might be considered conspecific. More evidence is awaited.

***Bombus (Ps.) cornutus* (Frison)**

cornutus (Frison, 1933:338 [*Psithyrus*])

pyramideus (Maa, 1948:19 [*Psithyrus*]) examined

acutisquameus (Maa, 1948:21 [*Psithyrus*]) examined

klapperichi (Pittioni, 1949:273 [*Psithyrus*]) examined, not of Pittioni, 1949:266 (= *B. picipes* Richards)

?canus (Tkalcü, 1989:42 [*Psithyrus*])

***Bombus (Ps.) expolitus* Tkalcü**

expolitus (Tkalcü, 1989:44 [*Psithyrus*]) examined

***Bombus (Ps.) turneri* (Richards)**

turneri (Richards, 1929a:141 [*Psithyrus*]) examined

?monozonus (Friese, 1931:304 [*Psithyrus*]) not of Friese, 1909:674 (= *B. lucorum* (Linnaeus))

?decoomani (Maa, 1948:26 [*Psithyrus*]) examined

?martensi (Tkalcü, 1974b:314 [*Psithyrus*]) (provisional synonym)

● TAXONOMIC STATUS. Several of these nominal taxa have been treated as separate species. However, aside from differences in colour pattern, they are closely similar in morphology. Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

***Bombus (Ps.) tibetanus* (Morawitz)**

tibetanus (Morawitz, 1886:202 [*Apathus*])

?latefasciatus (Friese, 1931:304 [*Psithyrus*])

***Bombus (Ps.) chinensis* (Morawitz)**

chineusis (Morawitz, 1890[April 30]:352 [*Apathus*])

morawitzi (Friese, 1905:516 [*Psithyrus*]) not of Radoszkowski, 1876:101 (= *B. morawitzi* Radoszkowski)

hönei (Bischoff, 1936:26 [*Psithyrus*]) not of Bischoff, 1936:10 (= *B. friseanus* Skorikov)

Bombus* (Ps.) *uovus* (Frison)novus* (Frison, 1933:340 [*Psithyrus*])*?nepalensis* (Tkalcü, 1974b:318 [*Psithyrus*]) examined***Bombus* (Ps.) *brauickii* (Radoszkowski)***Brauickii* (Radoszkowski, 1893:241 [*Psithyrus*]) examined*chloronotus* (Morawitz, 1894:6 [*Apathus*])*elisabethae* (Reinig, 1940:231 [*Psithyrus*]) examined*[branichii]* (Kim & Ito, 1987:32 [*Psithyrus*]) incorrect subsequent spelling]***Bombus* (Ps.) *rupestris* (Fabricius)***rupestris* (Fabricius, 1793:320 [*Apis*])*Pyrenaeus* (Lepeletier, 1832:375 [*Psithyrus*])*Interruptus* (Lepeletier, 1832:381 [*Psithyrus*])*armeniacus* (Reinig, 1970:77 [*Psithyrus*]) not of Radoszkowski, 1877b:202 (= *B. armeniacus* Radoszkowski)***Bombus* (Ps.) *ferganicus* (Radoszkowski)***ferganicus* (Radoszkowski, 1893:241 [*Psithyrus*]) examined*ochraceus* (Morawitz, 1894:5 [*Apathus*])*indicus* (Richards, 1929a:139) examined***Bombus* (Ps.) *morawitzianus* (Popov)***morawitzianus* (Popov, 1931:148,183 [*Psithyrus*]) examined*redikorzevi* (Popov, 1931:160,181 [*Psithyrus*])

○ NOMENCLATURE. Grütte (1937) regarded *B. morawitzianus* and *B. redikorzevi* as conspecific and, following the Principle of First Reviser (ICZN, 1985: Article 24), chose *B. morawitzianus* as the name for the species.

Bombus* (Ps.) *campestris* (Panzer)campestris* (Panzer, 1801(74):11 [*Apis*])*Varinus* (Lepeletier, 1832:381 [*Psithyrus*])*flavus* (Pérez, 1884:265 [*Psithyrus*])*flavo-thoracicus* (Hoffer, 1889:49 [*Psithyrus*])*?susteraei* (Tkalcü, 1959:251 [*Psithyrus*]) examined, not of May, 1944:267 (= *B. maxillosus* Klug) (provisional synonym)*?susteraianus* (Tkalcü, 1977:224 [*Psithyrus*]) replacement name for *susteraei* Tkalcü, 1959:251 (provisional synonym)

● TAXONOMIC STATUS. I am unaware of any reason (other than minor differences) why *B. campestris* and *B. susteraianus* should not be considered conspecific.

Bombus* (Ps.) *bellardii* (Gribodo)Bellardii* (Gribodo, 1892:108 [*Psithyrus*]) examined*pieli* (Maa, 1948:29 [*Psithyrus*]) examined, **new synonym**
tajinshanensis (Pittoni, 1949:277 [*Psithyrus*]) examined, not of Pittoni, 1949:244 (= *B. kuhlingensis* Cockerell), **new synonym**

● TAXONOMIC STATUS. *B. bellardii*, *B.ieli* and *B. tajinshanensis* are closely similar in morphology and I am unaware of any reason why these nominal taxa should not be considered conspecific.

○ NOMENCLATURE. For this species, the oldest available name is *B. bellardii*, which becomes the valid name. The only subsequent publications using the name *B.ieli* of which I am aware are by Maa (1948), Sakagami (1972), Tkalcü (1987) and Williams (1991), so this change of valid name is not a serious disruption of common usage.

Bombus* (Ps.) *norvegicus* (Sparre-Schneider)✱norvegicus* (Sparre-Schneider, 1918:40 [*Psithyrus*]) not of Friese, 1911:571 (= *B. monticola* Smith)*transbaicalicus* (Popov, 1927:269 [*Psithyrus*])

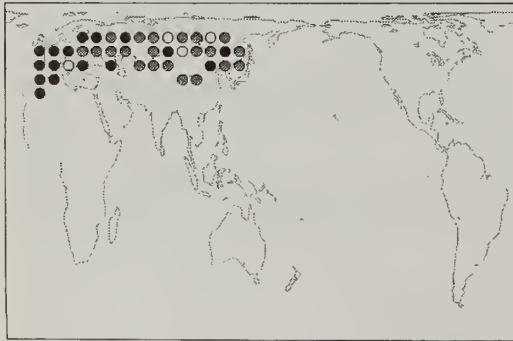
○ NOMENCLATURE. With *Psithyrus* regarded as being a subgenus of the genus *Bombus* (Williams, 1991, 1995), *P. norvegicus* Sparre-Schneider (1918) becomes a junior secondary homonym in *Bombus* of *B. lapponicus* var. *norvegicus* Friese (1911) (deemed subspecific, see ICZN, 1985: Article 45g(ii)), and therefore the name *P. norvegicus* Sparre-Schneider is invalid (ICZN, 1985: Article 57c). For this species, the oldest available name of which I am aware is *P. norvegicus* var. *transbaicalicus* Popov, 1927 (deemed to be subspecific, see ICZN, 1985: Article 45g(ii)), so *B. transbaicalicus* would become the valid name.

✱ APPLICATION TO ICZN. Although *B. transbaicalicus* is the oldest available name for this species, the name *B. norvegicus* has been in common use for the species since 1947 (e.g. Faester & Hammer, 1970; Delmas, 1976; Ito & Tadauchi, 1981; Pekkarinen *et al.*, 1981; Reinig, 1981; Løken & Framstad, 1983; Rasmont, 1983; Løken, 1984; Ito, 1985; Pekkarinen & Teräs, 1993; Rasmont *et al.*, 1995). It is suggested that, in the interests of stability, an application be made to ICZN to use its Plenary Power to suppress the senior homonym (ICZN, 1985: Article 79) (see the comments on *B. muscorum*). However, the consequence of this action would be that *norvegicus* Friese would no longer be available for a subspecies of *B. monticola*.

Bombus* (Ps.) *fernaldae* (Franklin)fernaldae* (Franklin, 1911:164 [*Psithyrus*]) examined

Bombus* (Ps.) *flavidus* Eversmannflavidus* Eversmann, 1852:131*lissonurus* (Thomson, 1872:49 [*Apathus*])

● TAXONOMIC STATUS. Rasmont (1988) reports that the Pyrenean population of *B. flavidus* is morphometrically distinct from the disjunct Scandinavian population (comparable distinctions are not known within its close relatives *B. norvegicus* and *B. sylvestris*, which share these areas of distribution). Nevertheless he continues to treat them as conspecific and I shall follow this, at least until further evidence in support of two separate species is available.

Bombus* (Ps.) *skorikovi* (Popov)skorikovi* (Popov, 1927:267 [*Psithyrus*]) examined*?gansuensis* (Popov, 1931:202 [*Psithyrus*])*?kuani* (Tkalcü, 1961b:362 [*Psithyrus*])***Bombus* (Ps.) *quadricolor* (Lepeletier)***Quadricolor* (Lepeletier, 1832:376 [*Psithyrus*])*globosus* (Eversmann, 1852:126 [*Psithyrus*])*meridionalis* (Richards, 1928b:351 [*Psithyrus*]) not ofDalla Torre, 1879:13 (= *B. hortorum* (Linnaeus))***Bombus* (Ps.) *sylvestris* (Lepeletier)***Sylvestris* (Lepeletier, 1832:377 [*Psithyrus*])*Brasiliensis* (Smith, 1854:385 [*Apathus*]) examined, not ofLepeletier, 1836:470 (= *B. brasiliensis* Lepeletier)*citrinus* (Schmiedeknecht, 1883[see Baker, 1996c:297]:23[407] [*Psithyrus*]) not of Smith, 1854:385(= *B. citrinus* (Smith))*[sylvestris]* (Dalla Torre, 1896:571 [*Psithyrus*]) incorrect subsequent spelling]**Subgenus *LAESOBOMBUS* Krüger***Bombus* (*Laesobombus*) Krüger, 1920:350, type-species*Bombus laesus* Morawitz by monotypy*Agrobombus* (*Laesobombus*) Skorikov, 1922b:20, type-species *Bombus laesus* Morawitz by monotypy*Agribombus* (*Laesibombus*) Skorikov, 1938a:145, unjustified emendation***Bombus* (Ls.) *laesus* Morawitz***laesus* Morawitz in Fedtschenko, 1875:3*Mocsáryi* Kriechbaumer, 1877:253*?maculidorsis* (Skorikov, 1922b:23 [*Agrobombus*]) not infrasubspecific after Panfilov, 1956:1328*?tianschanicus* Panfilov, 1956:1327 (provisional synonym)*ferrugifer* Reinig, 1971:158

● TAXONOMIC STATUS. Panfilov (1956) regarded *B. laesus*, *B. mocsaryi*, *B. maculidorsis* and *B. tianschanicus* as separate species, differing particularly in: (1) the colour of the pubescence on the thoracic dorsum; (2) the number of large punctures on the clypeus; (3) the strength of the median keel on gastral sternum VI; and (4) the length of the hair of the dorsum. However, from the material I have examined (collections in London, Beijing), these character states do not appear to be either discrete or strongly associated. Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

**Subgenus *ORIENTALIBOMBUS* Richards***Bombus* (*Orientalibombus*) Richards, 1929c:378, type-species *Bombus orientalis* Smith (= *Bombus haemorrhoidalis* Smith) by original designation*Bombus* (*Orientalobombus*) Kruseman, 1952:102, unjustified emendation***Bombus* (Or.) *funerarius* Smith***funerarius* Smith, 1852b:47, examined*priscus* (Frison, 1935:349 [*Brenus*])*birmanus* (Tkalcü, 1989:47 [*Orientalibombus*]) examined***Bombus* (Or.) *braccatus* Friese***braccatus* Friese, 1905:512, examined*metcalfi* (Frison, 1935:357 [*Brenus*]) examined***Bombus* (Or.) *haemorrhoidalis* Smith***haemorrhoidalis* Smith, 1852a:43*orientalis* Smith, 1854:402, examined*assamensis* Bingham, 1897:550, examined

montivolans Richards, 1929c:382, examined
semialbopleuralis (Tkalcü, 1974b:322 [*Orientalibombus*])
cinnamensis (Tkalcü, 1989:47 [*Orientalibombus*]) examined

● **TAXONOMIC STATUS.** Several of these nominal taxa have been treated as separate species, most recently in the case of *B. montivolans* [Burma to southern China] (e.g. Tkalcü, 1968b, 1989). However, aside from differences in colour pattern, they are all closely similar in morphology with a range of variation (Williams, 1991). Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.



Subgenus **EXILOBOMBUS** Skorikov

Mucidobombus (*Exilobombus*) Skorikov, 1922a:150, type-species *Mucidobombus exil* Skorikov (cited as *exilu.*) (= *Bombus exil* (Skorikov)) by monotypy
Megabombus (*Exiluobombus*) Milliron, 1973a:81, unjustified emendation

Bombus* (Ex.) *exil (Skorikov)

exilu. uov. (Skorikov, 1922a:150 [*Mucidobombus*]) [not a replacement name]
[exil] (Skorikov, 1931:216 [*Mucidobombus*]) incorrect subsequent spelling
exil (Milliron, 1961:56 [*Megabombus*]) justified emendation
[exilis] Richards, 1968:254, incorrect subsequent spelling
exil (Tkalcü, 1974a:42 [*Megabombus*]) unjustified emendation



Subgenus **THORACOBOMBUS** Dalla Torre

Bombus (*Thoracobombus*) Dalla Torre, 1880:40, type-

species *Apis sylvarum* Linnaeus (= *Bombus sylvarum* (Linnaeus)) by subsequent designation of Sandhouse, 1943:604

Bombus (*Clromobombus*) Dalla Torre, 1880:40, type-species *Apis muscorum* Linnaeus (= *Bombus muscorum* (Linnaeus)) by subsequent designation of Sandhouse, 1943:538

Bombus (*Agrobombus*) Vogt, 1911:52, type-species *Apis agrorum* Fabricius (= *Bombus pascuorum* (Scopoli)) by subsequent designation of Sandhouse, 1943:523

[*Agrabombus* Skorikov, 1914a:119, incorrect subsequent spelling]

Bombus (*Ruderariobombus*) Krüger, 1920:350, type-species *Apis ruderaria* Müller (= *Bombus ruderarius* (Müller)) by subsequent designation of Yarrow, 1971:27

Agrobombus (*Adventoribombus*) Skorikov, 1922a:150, type-species *Agrobombus adventor* Skorikov (= *Bombus filchnerae* Vogt) by subsequent designation of Sandhouse, 1943:522, **new synonym**

[*Agrobombus* (*Adventoribombus*) Skorikov, 1931:218, incorrect subsequent spelling]

Agribombus Skorikov, 1938a:145, unjustified emendation
[Boubus (*Thoracobombus*) Esmaili & Rastegar, 1974:52, incorrect subsequent spelling]

[*Boubus* (*Thoracibombus*) Schwarz *et al.*, 1996:197, incorrect subsequent spelling]

● **TAXONOMIC STATUS.** Richards (1968) treated *Thoracobombus* and *Adventoribombus* as separate subgenera, although he questioned whether they should be kept separate. I have followed Tkalcü (1974a) in treating *B. adventor* (= *B. filchnerae*) as part of a single subgenus *Thoracobombus*.

Bombus* (Th.) *filchnerae Vogt

Filchnerae Vogt, 1908:100, examined
adventor (Skorikov, 1914a:119 [*Agrabombus*])
lii Tkalcü, 1961b:355

Bombus* (Th.) *muscorum (Linnaeus)

Muscorum (Linnaeus, 1758:579 [*Apis*]) examined
pallidus Evans, 1901:47, not of Cresson, 1863:92 (= *B. pensylvanicus* (DeGeer))
[fulvofasciatus] Friese, 1905:520, infrasubspecific
laevis Vogt, 1909:63
?nigripes Pérez, 1909:158, not of Haliday in Curtis *et al.*, 1837:321 (= *B. dalibonii* Guérin-Méneville)
?pereziellus (Skorikov, 1922a:150 [*Agrobombus*]) replacement name for *nigripes* Pérez, 1909:158
?bannitus (Skorikov in Popov, 1930:98 [*Agrobombus*])
?liepetterseui Løken, 1973:152
celticus Yarrow, 1978:15, replacement name for *pallidus* Evans, 1901:47

● **TAXONOMIC STATUS.** *B. bannitus* (= *B. smithianus* of authors, a misidentification (= *B. pascuorum*)) has been regarded as a separate species by some authors (e.g. Richards, 1935; Tkalcü, 1987; Rasmont & Adamski, 1995) on the basis of its semi-melanic colour pattern and more coarsely sculptured surface of

gastral terga IV–V. However, Løken (1973: fig. 81) found no difference between these taxa in a morphometric study (other authors reporting no clear morphological differences include Richards, 1935; Alford, 1975; Pekkarinen, 1979; Rasmont, 1982; Baker, 1996a). Furthermore, I have collected many specimens with a range of intermediate colour patterns on the Isle of Skye in western Scotland. Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

B. pereziellus has also been regarded as a separate species by Rasmont & Adamski (1995), because of its dark colour pattern (even darker than *B. bannitus*, *B. pereziellus* has the thoracic dorsum black rather than red-brown, and has more black hairs on gastral tergum II, whereas these black hairs tend to be more frequent on tergum I for *B. bannitus*) and because it is endemic to the island of Corsica. Morphologically it was considered by Rasmont (1982) to show no perceptible differences from *B. muscorum* or *B. bannitus*. Furthermore, a male with a colour pattern apparently intermediate between *B. muscorum* and *B. pereziellus* is mentioned by Delmas (1976:271). Depending on the species concept embraced, some differences might be expected for a peripheral population such as this even if it were conspecific and I shall treat them as parts of a single variable species. Further evidence is awaited.

○ NOMENCLATURE. Richards (1935, 1968), Yarrow (1968) and Løken (1973) recognised that none of the admissible syntypes in the Linnean collection agreed with the traditional interpretation of *B. muscorum*, which is very rare in the parts of Sweden where Linnaeus collected (Richards, 1935; Løken, 1973; Day, 1979), but took no action. When Day (1979) came to fix the application of the name, he had no reason to believe that Linnaeus had not described his *A. muscorum* from the syntype specimen that was subsequently described as lectotype (= *B. humilis* Illiger).

To reaffirm the traditional usage of *B. muscorum*, a case was made to ICZN by Løken *et al.* (1994). This sought an Opinion from ICZN (ICZN, 1996) that set aside by use of its Plenary Power (ICZN, 1985: Articles 78b, 79) the lectotype designation for *A. muscorum* by Day from application of the Code (ICZN, 1985) and then designated a neotype (ICZN, 1996: 64) to conserve the traditional usage of the name for even the narrowest concept of the taxon (ICZN, 1985: Article 75).

Bombus (Th.) *anachoreta* (Skorikov)
anachoreta (Skorikov, 1914a:121 [*Agrobombus*])

Bombus (Th.) *opulentus* Smith
opulentus Smith, 1861:153, examined

Bombus (Th.) *zonatus* Smith
zonatus Smith, 1854:389

Bombus (Th.) *humilis* Illiger☼
fulvescens (Schrank, 1802:367 [*Apis*])
humilis Illiger, 1806:171
tristis Seidl, 1837:69
variabilis Schmiedeknecht, 1878:424, not of Cresson,
1872:284 (= *B. variabilis* (Cresson))
subbaicalensis Vogt, 1911:42,54

○ NOMENCLATURE. When Day (1979) came to fix the application of *A. muscorum* Linnaeus (see the comments on *B. muscorum*), he had no reason to believe that Linnaeus had not described this taxon from the syntype specimen that was subsequently described as lectotype (= *B. humilis* Illiger). This action brought *B. humilis* Illiger into subjective junior synonymy with *B. muscorum* (Linnaeus).

To reaffirm the traditional usage of *B. muscorum* and *B. humilis*, a case was made to ICZN by Løken *et al.* (1994). This sought an Opinion from ICZN (ICZN, 1996) that set aside by use of its Plenary Power (ICZN, 1985: Articles 78b, 79) the lectotype designation for *A. muscorum* by Day from application of the Code (ICZN, 1985) and then designated a neotype (ICZN, 1996: 64) to conserve the traditional usage of *B. muscorum* and *B. humilis* (ICZN, 1985: Article 75).

However, Warncke (1986) recognised *B. fulvescens* (Schrank) as questionably conspecific with *B. humilis*. I have seen no type specimens, but the description is consistent with this interpretation. *B. fulvescens* is therefore likely to be the oldest available name for this species.

☼ APPLICATION TO ICZN. Although *B. fulvescens* may be the oldest available name for the present interpretation of this species, the name *B. humilis* has been in common use for the species since 1947 (e.g. case and references in Løken *et al.*, 1994). In contrast, I know of no publications using the name *B. fulvescens* (Schrank) since 1947. Warncke (1986:98) followed the listing of this name with 'Art. 23b', which is a reference to purpose of the Principle of Priority (ICZN, 1985). I agree that, in the interests of stability, an application be made to ICZN to use its Plenary Power to suppress the unused senior synonym (ICZN, 1985: Article 79) (see the comments on *B. muscorum*).

Bombus (Th.) *deuteronymus* Schulz
senilis Smith, 1879:131, examined, not of Fabricius,
1775:382 (= *B. pascuorum* (Scopoli))
deuteronymus Schulz, 1906:267, replacement name for

senilis Smith, 1879:131
velox (Skorikov, 1914a:120 [*Agrobombus*])
superequester (Skorikov, 1914c:405 [*Agrobombus*])
infrasubspecific
superequester (Skorikov, 1925:116 [*Agrobombus*])
buerschii Pittioni, 1939b:1, examined

***Bombus (Th.) schrencki* Morawitz**

Schrencki Morawitz, 1881:123
Schrencki Morawitz, 1881:250, redescribed
konakovi Panfilov, 1956:1330

?*Bombus (Th.) honshuensis* (Tkalčič)

honshuensis (Tkalčič, 1968a:47 [*Megabombus*])

● TAXONOMIC STATUS. *B. honshuensis* and *B. schrencki* have allopatric distributions in northern Japan (Sakagami & Ishikawa, 1969; Ito & Munakata, 1979: fig. 6; Ito, 1993), with *B. honshuensis* being possibly a disjunct peripheral population of *B. schrencki*. The two taxa are closely similar, and yet despite some variation in morphology, apparently consistent differences have been described (Tkalčič, 1968a; Sakagami & Ishikawa, 1972). Nonetheless, some differences might be expected even if they were conspecific, depending on the species concept accepted (see the comments on *B. ruderatus*), so further evidence is awaited.

***Bombus (Th.) impetuosus* Smith**

impetuosus Smith, 1871:249, examined
Potanini Morawitz, 1890:350, **new synonym**
yuenmanensis Bischoff, 1936:14, examined
combai Tkalčič, 1961b:357, **new synonym**

● TAXONOMIC STATUS. The white-banded *B. potanini* is morphologically closely similar to the yellow-banded *B. impetuosus*. Some individuals from Sichuan are intermediate in colour pattern in that they have the pale bands of the thorax and gastral tergum I white, and the pale band of tergum II yellow. There is considerable variation in the male gonostylus, but this variation appears to overlap between the the colour forms and I shall treat them as parts of a single variable species. S.-f. Wang and J. Yao (*in litt.*) also believe that the two taxa may be conspecific. Further evidence is awaited.

***Bombus (Th.) remotus* (Tkalčič)**

remotus (Tkalčič, 1968a:45 [*Megabombus*]) examined

***Bombus (Th.) pseudobaicalensis* Vogt**

Pseudobaicalensis Vogt, 1911:43,53
gilvus (Skorikov, 1925:117 [*Agrobombus*])

***Bombus (Th.) hedini* Bischoff**

unicolor Friese, 1905:514, examined, not of Kriechbaumer, 1870:159 (= *B. maxillosus* Klug)
hedini Bischoff, 1936:15

***Bombus (Th.) ruderarius* (Müller)**

ruderaria (Müller, 1776:165 [*Apis*])
Derhamella (Kirby, 1802:363 [*Apis*]) examined
montanus Lepelletier, 1836:463
simulacris Radoszkowski, 1888:317, examined

***Bombus (Th.) inexpectatus* Tkalčič**

lutescens Krüger, 1939:105, not of Pérez, 1890:154 (= *B. flavidus* Eversmann)
inexpectatus (Tkalčič, 1963:187 [*Agrobombus*])
[inexpectatus (Reinig, 1981:161 [*Megabombus*]) incorrect subsequent spelling]

COMMENT. On the grounds of its peculiar morphology, *B. inexpectatus* has been suggested to be an obligate social parasite in colonies of other *Bombus* species, with *B. ruderarius* being the most likely host (Yarrow, 1970). As yet, there is no direct evidence for this behaviour (Rasmont, 1988). See the comments on the subgenus *Psithyrus* and on *B. hyperboreus*.

***Bombus (Th.) sylvarum* (Linnaeus)**

sylvarum (Linnaeus, 1761:425 [*Apis*]) examined
Daghestanicus Radoszkowski, 1877a:vii
Dagestanicus Radoszkowski, 1877b:211, redescribed

***Bombus (Th.) veteranus* (Fabricius)**

veterana (Fabricius, 1793:324 [*Apis*])
areuicola Thomson, 1872:31

***Bombus (Th.) mlokosievitzii* Radoszkowski**

Mlokosievitzii Radoszkowski, 1877a:viii
Mlokassewiczii Radoszkowski, 1877b:212, redescribed
pérezii Vogt, 1911:55, not of Schulthess-Rechberg, 1886:275 (= *B. pérezii* (Schulthess-Rechberg))
vogtiellus (Tkalčič, 1977:224 [*Megabombus*]) replacement name for *pérezii* Vogt, 1911:55
[mlokossowiczii (Reinig, 1981:161 [*Megabombus*]) incorrect subsequent spelling]

○ NOMENCLATURE. There are particularly many incorrect subsequent spellings of *B. mlokosievitzii*.

***Bombus (Th.) pascuorum* (Scopoli)**

Pascuorum (Scopoli, 1763:306 [*Apis*])
fenilis (Fabricius, 1775:382 [*Apis*])
agrorum (Fabricius, 1787:301 [*Apis*]) not of Schrank, 1781:397 (= *B. mesonucelus* Gerstaecker)
thoracicus Spinola, 1806:30

arcticus Dahlbom, 1832:50, not of Quenzel in Acerbi, 1802:253 (= *B. hyperboreus* Schönherr)
cognatus Stephens, 1846:17, examined
smithianus White, 1851:158

● **TAXONOMIC STATUS.** Warncke (1986) listed *B. cognatus* as a synonym of *B. muscorum*, possibly following Stephens (1846), who wrote of *B. cognatus*: 'Closely allied to *Bo. Muscorum*, of which the examples I possess may be immature specimens'. Pagliano (1995) listed *B. cognatus* as a species separate from both *B. muscorum* and *B. pascuorum*, but without any explanation.

Saunders (1896:366–367) wrote 'I have re-examined the type of *cognatus*, Steph., . . . F. Smith placed it in the British Museum collection. . . . Saunders considered this specimen to be conspecific with *B. agrorum* (Fabricius), continuing: 'It is certainly not the species known on the Continent as *cognatus*'.

A female in the NHM collection bears the following labels: (1) a red-edged printed 'Type'; (2) '*cognatus*,' in handwriting identical to that of F. Smith; (3) '= *agrorum* / I.H.H.Y.' in handwriting identical to that of I. Yarrow; (4) 'B.M. Type / HYM. / 17B.1163'. I have examined this specimen and am unaware of any reason why it should not be considered the type of *B. cognatus* and (ignoring minor differences in colour pattern) conspecific with *B. pascuorum*.

○ **NOMENCLATURE.** Løken (1973) listed *B. cognatus* Stephens, 1846, as *anomen nudum*, citing Sherborn (1925). However, the reference by Sherborn is to an earlier paper by Stephens (1829), so this does not affect the use of the name *B. cognatus* Stephens, 1846.



Subgenus **TRICORNIBOMBUS** Skorikov

Agrobombus (*Tricornibombus*) Skorikov, 1922a:151, type-species *Bombus tricornis* Radoszkowski by monotypy
Bombus (*Tricornibombus*) Tkalcü, 1960:70

Bombus* (Tr.) *tricornis Radoszkowski

tricornis Radoszkowski, 1888:319, examined

Bombus* (Tr.) *atripes Smith

atripes Smith, 1852a:44, examined

Bombus* (Tr.) *imitator Pittioni

imitator Pittioni, 1949:251, examined

flavescens Pittioni, 1949:254, not of Smith, 1852a:45 (= *B. flavescens* Smith)



Subgenus **FERVIDOBOMBUS** Skorikov

Fervidobombus Skorikov, 1922a:153, type-species *Apis fervida* Fabricius (= *Bombus fervidus* (Fabricius)) by subsequent designation of Frison, 1927:69

Bombus (*Fervidobombus*) Franklin, 1954:47

Bombus (*Digressobombus*) Laverty *et al.*, 1984:1051, type-species *Megabombus digressus* Milliron (= *Bombus digressus* (Milliron)) by original designation

● **TAXONOMIC STATUS.** The subgenus *Digressobombus* was described subsequent to Richards (1968). I have treated *Digressobombus* as part of a single subgenus *Fervidobombus* (Williams, 1995), as has Labougle (1990). While this study found no evidence for monophyly of the combined group, I believe that this is more likely (unpublished data) than monophyly of the subgenus *Fervidobombus* excluding *Digressobombus*.

COMMENT. This is the only early-diverging and large subgenus of bumble bees to occur in the New World other than the subgenus *Psithyrus*. Although it makes up only a small part of the fauna of America north of Mexico, it makes up most of the low- to mid-altitude bumblebee fauna of Central and South America. It also includes the only species of bumble bees genuinely occurring in tropical lowland wet forest (e.g. Moure & Sakagami, 1962; Milliron, 1973a; Cameron & Whitfield, 1996). The species with more temperate distributions appear to occupy similar habitats and show similar flower-depth preferences to species of subgenera such as *Thoracobombus* and *Megabombus* in the Old World.

Bombus* (Fv.) *fervidus (Fabricius)

fervida (Fabricius, 1798:274 [*Apis*])

?*Californicus* Smith, 1854:400, examined

Dumoucheli Radoszkowski, 1884:78

sonomae Howard, 1902:pl. II

● **TAXONOMIC STATUS.** *B. fervidus* and *B.*

californicus have been regarded both as conspecific (e.g. Milliron, 1973a; Labougle, 1990) and as separate species (e.g. Franklin, 1913; Stephen, 1957; Thorp *et al.*, 1983; Poole, 1996). Both Franklin (1913:239) and Stephen (1957) also considered the possibility that they are conspecific as quite reasonable.

Many specimens from the north west of North America show a reduction in the extent of the yellow bands on the scutellum and gastral terga I–III and appear to be intermediate or recombinant individuals. Indeed, Stephen's (1957:32) figure 2 shows several patterns that could represent a continuum in variation between the two forms. Thorp *et al.* (1983) found no intermediate females in California, although some of the males of *B. californicus* were said to approach the pattern of *B. fervidus*.

In view of the existence of apparent intermediates between these nominal taxa in at least part of their range, they are treated here as likely to be conspecific. More evidence is awaited.

○ NOMENCLATURE. *Apis feruida* is the original spelling in Fabricius (1798). The orthography of this publication employs 'u' in place of 'v' widely, a common practice of the period. This convention has since changed and subsequent authors have consistently used 'v' for *B. fervidus*.

In fact, whatever the interpretation of the Code, pragmatically it matters little which spelling of *fervidus* is used unless either of the spellings were to be published as the name of another taxon in *Bombus*. See the comments on the spelling of *B. pensylvanicus*.

Bombus (Fv.) *pensylvanicus* (DeGeer)

pensylvanica (DeGeer, 1773:575 [*Apis*])

americanorum Fabricius, 1804:346

?*sondus* Say, 1837:413

pallidus Cresson, 1863:92

Pensylvanicus Cresson, 1863:94

flavodorsalis Franklin, 1913:409

pennsylvanicus Hurd, 1979:2204, unjustified emendation

● TAXONOMIC STATUS. *B. pensylvanicus* and *B. sonorus* have been regarded both as conspecific (e.g. Milliron, 1973a; Labougle *et al.*, 1985; Labougle, 1990; Poole, 1996) and as separate species (e.g. Franklin, 1913 [but see p. 239]; Stephen, 1957; Thorp *et al.*, 1983; S. Cameron *in litt.*).

From the few males from the United States (not Mexico) that I have examined in detail, there appear to be subtle differences in the male genitalia (e.g. in the shape of the penis valve head). However, Labougle (1990) reports that the two 'forms are geographically intermixed in México, and chromatically intermediate specimens occur, mainly in northeastern México and southwestern Texas'. He went on to say that 'In fact, it is sometimes difficult to place a Mexican specimen in either subspecies because there are specimens with the

coloration of the scutellum and the punctuation of the clypeus intermediate between the two taxa. Average differences of certain proportions are found . . . but do not differentiate all specimens'. G. Chavarría (pers. com.) also believes that intermediate specimens occur in Mexico and that they are conspecific. Taking an extreme viewpoint, it is even possible to see the 'typical' *B. sonorus* colour pattern as intermediate between *B. pensylvanicus* (in the strict sense) and the extreme pale form that has the thoracic dorsum and gastral tergum I entirely yellow (*flavodorsalis*, see Thorp *et al.*, 1983: fig. 137b).

In view of the existence of apparent intermediates between these nominal taxa in at least part of their range, they are treated here as likely to be conspecific. More evidence is awaited.

○ NOMENCLATURE. *Apis pensylvanica* is the original spelling in DeGeer (1773). The orthography of this publication employs 'j' in place of 's' widely, a common practice of the period. This convention has since changed and subsequent authors (e.g. Cresson, 1863) have consistently used 's' for *B. pensylvanicus*.

Technically, according to the Code (ICZN, 1985: Article 32b), *pensylvanicus* with just two 'n's is the correct original spelling, to be preserved unaltered unless it is demonstrably incorrect under Article 32c. Article 32c(ii) states that clear evidence of an inadvertent error is only admissible if it lies within the original publication, *without recourse to any external source of information* (DeGeer, 1773, spelled *Penſylvanie* and *penſylvanica* consistently in this way). Any intentional change to that spelling in a subsequent publication is an unjustified emendation under Article 33b(iii).

In fact, whatever the interpretation of the Code, pragmatically it matters little which spelling of *pensylvanicus* is used unless either of the spellings were to be published as the name for another taxon in *Bombus*. No doubt many will prefer to use *B. pennsylvanicus*, although the name does appear as *B. pensylvanicus* in the recent checklist by Poole (1996) (and by analogy, the similar spelling of *Vespula pensylvanica* (Saussure) has been accepted, e.g. by Akre *et al.*, 1980; Edwards, 1980).

COMMENT. This species was deliberately introduced into the Philippines, but is not known to have persisted (Frison, 1925b).

Bombus (Fv.) *excellens* Smith

excellens Smith, 1879:133, examined

Bombus (Fv.) *dahlbomii* Guérin-Ménéville

Dahlbomii Guérin-Ménéville, [1835, see Cowan, 1971:29]:pl.75

nigripes Haliday in Curtis *et al.*, 1836:321

○ NOMENCLATURE. Cowan (1971), considering Guérin-Méneville's insect volume, states that 'it is quite certain that valid publication [of the *Insectes* text] under the International Code of Nomenclature did not take place until August or September 1844.' However, he lists plate 75, on which *B. dahlbomii* appears as figure 3 together with a legend containing the name, as having been published in livraison 39 in June 1835. This meets the criteria for valid publication (ICZN, 1985: Article 8). Therefore *B. dahlbomii* is the oldest available name for this species.

***Bombus (Fv.) morio* (Swederus)**

morio (Swederus, 1787:283 [Apis]) examined
velutinus Illiger, 1806:175
violaceus Lepelletier, 1836:473
carbonarius Handlirsch, 1888:241, not of Menge, 1856:27 [fossil]
Kohli Cockerell, 1906:75, replacement name for
carbonarius Handlirsch, 1888:241

***Bombus (Fv.) diligens* Smith**

diligens Smith, 1861:154, examined
dolichocephalus Handlirsch, 1888:244

***Bombus (Fv.) opifex* Smith**

opifex Smith, 1879:133, examined

***Bombus (Fv.) rubriventris* Lepelletier**

rubriventris Lepelletier, 1836:472, examined

● TAXONOMIC STATUS. *B. rubriventris* is known from a single female specimen from 'St. Domingue' (?= São Domingos, Goiás) (Milliron, 1973a). This specimen has dark brown wings and the pubescence is black, except that most of the hairs of the thorax are grey-tipped, and the hairs of gastral terga II–IV are bright 'coppery' red.

This colour pattern resembles the Andean *B. excellens*, although the pubescence of *B. rubriventris* is much shorter and more even; the oculo-malar area is nearly square rather than nearly twice as long as the basal breadth of mandible; and tergum VI is raised subapically. Franklin (1913) had not seen *B. rubriventris* but suggested that it was probably a 'freak specimen' of *B. carolinus* (a misidentification, = *B. excellens*). Milliron (1973a) had examined *B. rubriventris* and considered the morphological characters to be very much like those of *B. bellicosus*. However, *B. rubriventris* can be distinguished by the much finer punctures in the centre of the clypeus and by an absence of a median ridge on tergum VI. I consider *B. rubriventris* to be more similar in these characters to *B. opifex*, although it can be distin-

guished from that species by a pair of characteristically slightly recessed bands of fine punctures extending anteriorly from the ocello-ocular areas and by a shallow median groove in the subapically raised area of tergum VI.

The colour pattern is very distinctive among non-Andean bumble bees in South America and does not appear to be the result of abnormal colour development. The specimen has had the gaster glued back into place, although the characters of both the head and gaster appear to be distinctive, so there is no reason to believe that the specimen is a composite and not genuine.

COMMENT. Milliron (1973a) researched the history of this specimen and believed that it may have been collected as early as 1800. He concluded that it was probably a highland species from southeastern Brazil and that it may now be extinct. If so, and accepting that it is very difficult to establish the absence of a species, this would be one of the few known cases of complete extinction of an insect species.

***Bombus (Fv.) bellicosus* Smith**

thoracicus Sichel, 1862:121, not of Spinola, 1806:30 (= *B. pascuorum* (Scopoli))
bellicosus Smith, 1879:131, examined
Emiliae Dalla Torre, 1890:139, replacement name for
thoracicus Sichel, 1862:121

***Bombus (Fv.) pullatus* Franklin**

pullatus Franklin, 1913:122

***Bombus (Fv.) transversalis* (Olivier)**

transversalis (Olivier, 1789:65 [Apis])
Cajennensis (Fabricius, 1798:273 [Apis])
incanum Franklin, 1913:131

***Bombus (Fv.) atratus* Franklin** ♂

azurea (Christ, 1791:129 [Apis])
?atratus Franklin, 1913:118, not of Friese, 1911:572 (= *B. mucidus* Gerstaecker) (provisional synonym)
?niger Franklin, 1913:120, examined (provisional synonym)
?nigriventris Friese, 1913:87 (provisional synonym)

● TAXONOMIC STATUS. At least four species of the subgenus *Fervidobombus* from Central and South America have many individuals for which the pubescence is almost entirely black. The genitalia of the males are quite distinctive, but association of the conspecific females with these males has caused problems.

In the original description of *B. niger*, Franklin stated that '*atratus* is possibly the male of *niger*' (p.

121), whereas in the original description of *B. atratus* he stated both that '*Niger* may represent the females of this species' (p. 118) and that 'This may be the true male of *kohli*' (p. 119). *B. niger* was described from a syntype series of four queens and four workers, of which one queen in the Smithsonian collection carries, amongst others, a red label 'LECTOTYPE / *Bombus* / *niger* Franklin / H.E. Milliron '59' and a label 'Boquete / Chiriqui'. This Central American locality was mentioned by Franklin, but is outside the known distribution of the species (Milliron, 1973a) to which the specimen belongs. In my opinion, this lectotype of *B. niger* is not conspecific with *B. pullatus* (contrary to the suggestion by Labougle, 1990, see also Milliron, 1962) but rather is conspecific with *B. atratus* Franklin.

Another possibility is that this variable species is the *Apis azurea* of Christ (1791). I know of no type specimens and the type locality was said to be in Africa ('1st in Afrika am Vorgebürg der guten Hofnung zu Haus'). The description and figure of the colour pattern do not agree with any African bees that I have been able to trace, but do resemble closely the yellow-banded individuals of the South American *B. niger*, the Central American *B. medius* Cresson, and the South American *B. transversalis* (Olivier) (although for the last named species the yellow bands on the thorax are usually broader). Among the specimens to hand, the wings do appear slightly more 'Schwarzblau' for *B. niger*, as described for *A. azurea*, although these grounds seem slim justification from which to establish the application of a name.

○ NOMENCLATURE. *B. azureus* is possibly the oldest available name for this species.

Milliron (1962), without mention of the name *B. azureus*, first regarded *B. atratus* and *B. niger* as conspecific and, following the Principle of First Reviser (ICZN, 1985: Article 24), chose *B. atratus* as the valid name for the species.

Unfortunately, *B. atratus* Franklin, 1913, is a junior primary homonym of *B. mucidus* var. *atratus* Friese, 1911 (deemed to be subspecific, see ICZN, 1985: Article 45g(ii)), therefore the name *B. atratus* Franklin is invalid (ICZN, 1985: Article 57b).

✱ APPLICATION TO ICZN. The name *B. azureus* has not been used since the original publication. The name *B. atratus* has been used for this species since 1947 (e.g. Moure & Sakagami, 1962; Sakagami & Zucchi, 1965; Sakagami *et al.*, 1967; Milliron, 1971, 1973a; Sakagami, 1976; Ito, 1985; Labougle, 1990; Varela, 1992; Silveira & Cure, 1993). It is suggested that, in the interests of stability (ICZN, 1985: Article 23b), an application be made to ICZN to use its Plenary Power to suppress both the unused senior synonym (ICZN, 1985: Article 79) and the senior homonym. This would achieve both an unambiguous, valid name for this species (see the comments on *B. muscorum*) and also

help to protect the validity of the names *B. medius* and *B. transversalis* from future change. However, the consequence of this action would be that *atratus* Friese would no longer be available for a subspecies of *B. mucidus*.

***Bombus* (Fv.) *digressus* (Milliron)**

digressus (Milliron, 1962:730 [*Megabombus*]) examined

***Bombus* (Fv.) *brasiliensis* Lepeletier**

brasiliensis Lepeletier, 1836:470, examined

***Bombus* (Fv.) *steindachneri* Handlirsch**

Steindachneri Handlirsch, 1888:239

● TAXONOMIC STATUS. *B. medius* and *B. steindachneri* have been regarded both as separate species (Milliron, 1973a; Labougle, 1990) and as conspecific (G. Chavarría, pers. com.).

Labougle (1990) reports that 'Although the chromatic differences between *B. medius* and *B. steindachneri* are conspicuous, the male genitalia are extremely similar'. Labougle listed four character differences from the male genitalia and I can confirm two of these: (1) that the head of the penis valve of *B. steindachneri* has fewer fine teeth or serrations; and (2) that the interior process of the volsella (misinterpreted as the preapical tooth of the 'gonostylus'; for discussion of homologies see Williams, 1991) of *B. steindachneri* is narrower. However, I have examined only a few males and these characters might be expected to vary among other individuals. Labougle (1990) continued: 'The lack of chromatic and morphological intermediates supports the idea of two different species'.

Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as two separate species.

***Bombus* (Fv.) *medius* Cresson**

medius Cresson, 1863:97

***Bombus* (Fv.) *weisi* Friese**

laboriosus Smith, 1861:153, examined, not of Fabricius, 1804:352 (= *Emphoropsis laboriosus* (Fabricius))

weisi Friese, 1903:253, examined

nigrodorsalis Franklin, 1907:90

○ NOMENCLATURE. The lectotype female of *B. weisi* by designation of Milliron (1960:98) was recognised as conspecific with *B. nigrodorsalis* by Labougle (1990) (I have examined the lectotype of *B. weisi* at the MNHU, Berlin, and agree with Labougle). He then

used *B. weisi* (the oldest available name) as the valid name for this species. However, a case could be made in favour of the use of either name.

For Labougles's (1990) use of this previously unused senior synonym to be considered by ICZN as a *prima facie* case of upsetting the use of a long-accepted name in its accustomed meaning (ICZN, 1985: Article 23b), the name *B. weisi* should not have been used in this sense in the preceding fifty years; and at least five authors should have used the junior name, *B. nigrodorsalis*, in at least ten publications during the same period (ICZN, 1985: Article 79c). As far as I am aware, no other admissible publications have used *B. weisi* (Williams, 1995, disclaimed any nomenclatural action in a list of names for material examined), although publications using the junior name *B. nigrodorsalis* Franklin for this species since 1947 are more common, including Milliron (1961, 1962, 1971, 1973a), Laverty *et al.* (1984), Labougles *et al.* (1985), Williams (1985b) and Asperen de Boer (1992b). Other such references may exist, therefore this may be seen as a borderline case, requiring an application to be made to ICZN to use its Plenary Power if suppression of the unused senior synonym, *B. weisi*, is required (see the comments on *B. muscorum*).

On the other hand, a change of valid name from *B. nigrodorsalis* to *B. weisi* does not appear to be a serious disruption of common usage, so there is no obvious need for action to retain *B. nigrodorsalis* and I have continued to use *B. weisi*.

***Bombus* (Fv.) *trinominatus* Dalla Torre**

modestus Smith, 1861:153, examined, not of Eversmann, 1852:134 (= *B. modestus* Eversmann)
trinominatus Dalla Torre, 1890:139, replacement name for *modestus* Smith, 1861:153
xelajuensis Asperen de Boer, 1992b:162, examined (provisional synonym)

● **TAXONOMIC STATUS.** The description of *B. xelajuensis* shows that this nominal taxon, known from a single location, diverges only slightly in colour pattern and morphology from the otherwise restricted and uncommon mountain species *B. trinominatus*. Therefore it seems most likely to be conspecific with *B. trinominatus*, with a slightly different colour pattern. However, the information available at present is not conclusive, and it remains possible that it represents a separate species, and further evidence is awaited.

***Bombus* (Fv.) *mexicanus* Cresson**

mexicanus Cresson, 1878:187

***Bombus* (Fv.) *brevivillus* Franklin**

brevivillus Franklin, 1913:119

?*abditus* (Tkalčū, 1966:271 [*Megabombus*])

● **TAXONOMIC STATUS.** The single known female of *B. abditus* was described as originating from 'Rep. de Guinée Beyla' (equatorial Africa). However, it is indistinguishable from *B. brevivillus* according to Sakagami (1976:427) and probably represents an introduced or mislabelled individual (Michener, 1979).



Subgenus *SENEXIBOMBUS* Frison

Bremus (*Senexibombus*) Frison, 1930:3, type-species

Bombus senex Vollenhoven by original designation

[*Bombus* (*Senecibombus*) Kruseman, 1952:101 incorrect subsequent spelling]

Bombus (*Senexibombus*) Richards, 1968:217

***Bombus* (Sx.) *kulingensis* Cockerell**

kulingensis Cockerell, 1917:266

tajushanensis Pittioni, 1949:244

***Bombus* (Sx.) *bicoloratus* Smith**

bicoloratus Smith, 1879:132, examined

***Bombus* (Sx.) *senex* Vollenhoven**

Senex Vollenhoven, 1873:229

***Bombus* (Sx.) *irisanensis* Cockerell**

irisanensis Cockerell, 1910a:416, examined



Subgenus **DIVERSOBOMBUS** Skorikov

Bombus (Diversobombus) Skorikov, 1914c:406, type-species *Bombus diversus* Smith by subsequent designation of Sandhouse, 1943:546

Diversibombus Skorikov, 1938b:2, unjustified emendation

***Bombus (Dv.) trifasciatus* Smith**

trifasciatus Smith, 1852a:43, examined

montivagus Smith, 1878:168, examined

montivagus Smith, 1879:131, redescribed

?*wilemani* Cockerell, 1911:100, examined

albopleuralis Friese, 1916:108, examined

?*maxwelli* Pendlebury, 1923:67, examined

mimeticus Richards, 1931b:529, examined

malaisei (Skorikov, 1938b:2 [*Diversibombus*]) not of

Bischoff, 1930:4 (= *B. sporadicus* Nylander)

atropygus (Tkalčü, 1989:58 [*Megabombus*]) examined

● **TAXONOMIC STATUS.** Several of these nominal taxa have been treated as separate species, for example as *B. albopleuralis* (= *B. mimeticus*) [Himalaya], *B. montivagus* [northern Burma to southern China], *B. maxwelli* [Peninsular Malaysia] and *B. wilemani* [Taiwan] (Tkalčü, 1968b, 1989). However, aside from differences in colour pattern (Fig. 13), they are closely similar in morphology and show a range of variation (Williams, 1991). Until more evidence to the contrary is available from critical studies of patterns of variation, I shall continue to treat them as parts of a single variable species.

***Bombus (Dv.) longipes* Friese**

longipes Friese, 1905:511

hummeli Bischoff, 1936:18, examined

***Bombus (Dv.) diversus* Smith**

diversus Smith, 1869:207, examined

tersatus Smith, 1869:207, examined

○ **NOMENCLATURE.** Tkalčü (1965) first explicitly regarded *B. diversus* and *B. tersatus* as conspecific and, following the Principle of First Reviser (ICZN, 1985: Article 24), chose *B. diversus* as the valid name for the species.

***Bombus (Dv.) ussurensis* Radoszkowski**

Ussurensis Radoszkowski, 1877b:196

[*ussuriensis* Morawitz, 1881:254, incorrect subsequent spelling]



Subgenus **MEGABOMBUS** Dalla Torre

Bombus (Megabombus) Dalla Torre, 1880:40, type-species *Bombus ligusticus* Spinola (= *Bombus argillaceus* (Scopoli)) by monotypy

Bombus (Megabombus) Schulz, 1906:267, unjustified emendation

Bombus (Hortobombus) Vogt, 1911:56, type-species *Apis hortorum* Linnaeus (= *Bombus hortorum* (Linnaeus)) by subsequent designation of Sandhouse, 1943:559

Bombus (Odontobombus) Krüger, 1917:61.65 (proposed as a section name but stated by Milliron, 1961:53, to be equivalent to his concept of the subgenus *Megabombus* Dalla Torre), type-species *Apis argillacea* Scopoli (= *Bombus argillaceus* (Scopoli)) by subsequent designation of Williams, 1995:339

[*Nortobombus* Skorikov, 1922b:map 3, incorrect subsequent spelling]

Hortibombus Skorikov, 1938a:146, unjustified emendation

***Bombus (Mg.) supremus* Morawitz**

suprenus Morawitz, 1886:196

linguarius Morawitz, 1890:351

***Bombus (Mg.) gerstaeckeri* Morawitz**

Gerstäckeri Morawitz, 1881:242

Gerstaeckeri Hoffer, 1883:55, mandatory correction (ICZN, 1985: Article 32d)

***Bombus (Mg.) consobrinus* Dahlbom**

consobrinus Dahlbom, 1832:49

***Bombus (Mg.) tichenkoi* (Skorikov)**

[*tichenkoi* (Skorikov, 1922a:156 [*Hortobombus*]) published without description]

tichenkoi (Skorikov, 1925:115 [*Hortobombus*])

?yezoensis Matsumura, 1932:pl. 1

?przewalskiellus (Skorikov, 1933a:59 [*Hortobombus*])

kurileusis Sakagami, 1954:92

● **TAXONOMIC STATUS.** *B. tichenkoi* and *B. yezoensis* have apparently been regarded both as conspecific and as separate species.

Sakagami (1954) described *kurileusis* as a (semi-melanic) subspecies of what he called '*B. tersatus*' (a misidentification, = *B. diversus*). Following Tkalcü (1962), Sakagami subsequently identified his '*B. tersatus*' as *B. yezoensis* (Ito & Sakagami, 1980). In this later paper he went on to recognise *kurileusis* as conspecific with *B. tichenkoi*, but then, despite having regarded *kurileusis* as a subspecies of what he now believed to be *B. yezoensis* in the earlier paper, listed *B. tichenkoi* as a species separate from *B. yezoensis*. The apparent contradiction was not explained, although morphological comparisons between these taxa, *B. argillaceus* and *B. sushkini* were tabulated (which show primarily that *B. argillaceus* is very different). He even noted the allopatric distributions of *B. tichenkoi* and *B. yezoensis* between the northern and southern Kurile Islands and the 'resemblance of *tichenkoi* and dark individuals of *yezoensis*, especially in workers.'

Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat *B. tichenkoi* and *B. yezoensis* as parts of a single variable species.

Bombus (Mg.) *sushkini* (Skorikov)

[*saltuarius* (Skorikov, 1922a:156 [*Hortobombus*]) published without description]

sushkini (Skorikov, 1931:235 [*Hortobombus*]) examined
saltuarius (Skorikov, 1931:235 [*Hortobombus*])

● **TAXONOMIC STATUS.** *B. sushkini* and *B. saltuarius* have been regarded both as conspecific (Bischoff, 1936) and as separate species (Skorikov, 1931; Tkalcü, 1974a). I have as yet seen no evidence that more than one species is involved. More evidence is awaited.

○ **NOMENCLATURE.** Skorikov (1931) provided the first valid publication of the names *B. sushkini* and *B. saltuarius* as two separate species. Subsequently, Bischoff (1936) regarded the two as conspecific and, following the Principle of First Reviser (ICZN, 1985: Article 24), chose *B. sushkini* as the valid name for the species.

Bombus (Mg.) *portchinsky* Radoszkowski

Portchinskij Radoszkowski, 1883:208

Portchinsky Radoszkowski, 1883:208[210], 209[211], 210[212]

○ **NOMENCLATURE.** Radoszkowski (1883) published two different spellings of *B. portchinsky*,

repeating this second form several times (page numbers 207 and 208 are repeated twice for different pages, so the two spellings do not occur on the same page). Precedence of the correct original spelling should be determined using the Principle of the First Reviser (ICZN, 1985: Article 24), but to date I have not found an author who has correctly cited both names and then chosen one in precedence to the other (there are many incorrect subsequent spellings, e.g. Dalla Torre, 1896). Since the second form of the name has been used more recently (e.g. Baker, 1996b), I suggest that it should be given precedence. This form is a simple noun in apposition and so retains the same ending whatever the gender of the generic name with which it is combined (ICZN, 1985: Article 31b(ii)).

Bombus (Mg.) *hortorum* (Linnaeus)

hortorum (Linnaeus, 1761:424 [*Apis*]) examined

meridionalis Dalla Torre, 1879:13

hispanicus Pittioni, 1939c:244, not of Friese, 1911:571 (= *B. monticola* Smith)

asturiensis (Tkalcü, 1975:181 [*Megabombus*]) replacement name for *hispanicus* Pittioni, 1939c:244

?*reinigiellus* (Rasmont, 1983:43 [*Megabombus*])

● **TAXONOMIC STATUS.** The Spanish *B. asturiensis* has been considered a separate species from *B. hortorum* by Rasmont (1983, 1988), although they have been treated as conspecific by Pittioni (1939c), Tkalcü (1975), Ormosa (1986a, 1986b, 1991), Castro (1988, 1993) and, more recently, by Rasmont *et al.* (1995). The two taxa are closely similar.

The Spanish *B. reinigiellus* has also been considered both as conspecific with *B. hortorum* (Castro, 1987) and as a separate species (e.g. Rasmont, 1983; Castro, 1988; Ormosa, 1991). The two taxa are allopatric (Rasmont, 1983), with *B. reinigiellus* being narrowly restricted to the Sierra Nevada of Spain, possibly as a disjunct peripheral population. *B. reinigiellus* is closely similar to *B. hortorum*, although subtle differences in characters of colour and morphology have been described (e.g. Rasmont, 1983; Castro, 1988; Ormosa, 1991). From the material I have examined, the morphological differences appear to be analogous to the variation between mainland and island populations of *B. terrestris* (see the comments on *B. terrestris*).

Depending upon the species concept embraced, such subtle differences as those between *B. reinigiellus* and *B. hortorum* might be expected even within a single population and I shall treat all three taxa as conspecific for the present. More evidence is awaited.

COMMENT. *B. hortorum* has been introduced into New Zealand (e.g. Gurr, 1957; Macfarlane & Gurr, 1995) (see the comments on *B. ruderatus*, *B. subterraneus* and *B. terrestris*). It occurs in Iceland, where it has also probably been introduced (Prýs-Jones *et al.*, 1981) (see the comments on *B. lucorum*).

Bombus* (Mg.) *argillaceus (Scopoli)

Argillacea (Scopoli, 1763:305 [*Apis*])
ligusticus Spinola, 1806:29

?*Bombus* (Mg.) *ruderatus* (Fabricius)

ruderata (Fabricius, 1775:380 [*Apis*]) examined
Perniger (Harris, 1776:131 [*Apis*])
villarricaensis Asperen de Boer, 1992a:133

● TAXONOMIC STATUS. *B. argillaceus* and *B. ruderatus* are similar in most characters and differ principally in the colour patterns of the queens (e.g. Reinig, 1939; Fig. 11). Scholl, Obrecht & Zimmermann (1992) found that hybrid queens between *B. argillaceus* and *B. ruderatus* do occur in parts of southeastern France, but are very rare. Whether or not the taxa on either side of this hybrid zone are considered to be separate species therefore depends on which species concept is preferred. Because Scholl, Obrecht & Zimmermann (1992) estimated that only slight gene flow is occurring, I shall continue to treat them as separate species.

COMMENT. This species has been introduced into New Zealand (e.g. Gurr, 1957; Macfarlane & Gurr, 1995) (see the comments on *B. hortorum*, *B. subterraneus* and *B. terrestris*) and Chile (Arretz & Macfarlane, 1982; Asperen de Boer, 1993b). *B. ruderatus* also occurs on the Azores (which have never had a continental connection), where it may be presumed to be an introduction (Yarrow, 1967).

Bombus* (Mg.) *czerskii Skorikov

czerskii Skorikov, 1910b:413, examined

Bombus* (Mg.) *koreanus (Skorikov)

koreanus (Skorikov, 1933a:59 [*Hortobombus*])
pekingensis Bischoff, 1936:21, examined
?notocastaneus Tkalcü, 1961a:52 (provisional synonym)

● TAXONOMIC STATUS. *B. notocastaneus* was described from a single male from Hubei. From the description, it appears most likely to be conspecific with *B. koreanus*.

Bombus* (Mg.) *melanopoda Cockerell

melanopoda Cockerell, 1910a:416, examined

● TAXONOMIC STATUS. *B. melanopoda* is known from a single female specimen (labelled 'Sumatra', reverse '92.182.') in the NHM collection in London.

According to the accessions catalogue, the number on the label of this specimen refers to 8 Hymenoptera presented in November 1892 by H. O. Forbes. The area of origin is given as Borneo, although this has

been crossed out and Sumatra added. Forbes' (1885) account of his travels of 1878–1883 in Indonesia shows that he did not visit Borneo, although he did visit the mountains of southern Sumatra. There is no direct account of the collection of this specimen, although he recorded bees from at least three possible localities at higher altitudes: first, in late 1880 he climbed Gunung Tenggamas, where he recorded (p. 159) 'a few bees' at 7200 ft (2160 m); second, in 1881 he visited Gunung Dempa, where he recorded (p. 208) 'a fine grey-haired humble-bee (*Bombus senex*)' (identification by Forbes) between 7000–7700 ft (2100–2310 m); and later in the same year, near the summit of Gunung Kaba (1983 m), he recorded again (p. 228) 'A large humble-bee (*Bombus senex*)'.

B. melanopoda appears to be a morphologically distinct species. It can be distinguished from the only other long-tongued bumblebee species known from Sumatra, *B. senex*, by the longer oculo-malar area of *B. melanopoda*, which is more than 1.5 times longer than the basal breadth of the mandible. Otherwise, the most closely related long-tongued bumble bee in any neighbouring area is *B. trifasciatus* from the Cameron Highlands of Peninsular Malaysia. However, like most queens of the subgenus *Megabombus*, the holotype of *B. melanopoda* is easily distinguished by its narrow longitudinal median groove subapically on gastral tergum VI (for *B. trifasciatus* this area is uniformly convex). The colour pattern of the *B. melanopoda* female is predominantly black, but the hairs of terga IV–V are very slightly paler, so there is some similarity to the darkest queens of *B. koreanus*, which have this pubescence brownish cream. However, unlike the few queens of *B. koreanus* available to me, the type of *B. melanopoda* has the unpunctured areas around the ocelli extending to less than half the ocello-ocular distance; the dorsal furrow of the gena (between the vertex and the post-ocular area) is strongly marked anteriorly; and the dorsal face of the labral tubercles (the face adjacent to the clypeus) is more sharply separated from the anterior ventral face and more densely marked by moderate-sized punctures.

Since no further individuals have been found, the possibility that the holotype of *B. melanopoda* is a mislabelled melanic specimen of another species of the subgenus *Megabombus* ought to be explored, perhaps initially through a morphometric analysis.

COMMENT. Like most other Sumatran bumble bees (with the notable exception of the extensively greyish-white queens of *B. senex*, see Sianturi *et al.*, 1995), the holotype of *B. melanopoda* is almost entirely black. It is likely that females of this species would be particularly easily mistaken for black individuals of *B. senex* (although males of *B. melanopoda* might be paler, as for *B. koreanus*).

***Bombus (Mg.) securus* (Frison)**

securus (Frison, 1935:346 [*Bremus*]) examined
yuenanicus Bischoff, 1936:23, examined

***Bombus (Mg.) religiosus* (Frison)**

religiosus (Frison, 1935:344 [*Bremus*]) examined

**Subgenus RHODOBOMBUS Dalla Torre**

Bombus (Rhodobombus) Dalla Torre, 1880:40, type-species *Bremus pomorum* Panzer (= *Bombus pomorum* (Panzer)) by subsequent designation of Sandhouse, 1943:596

Bombus (Pomobombus) Krüger, 1917:65, type-species *Bremus pomorum* Panzer (= *Bombus pomorum* (Panzer)) by subsequent designation of Sandhouse, 1943:589
Pomibombus Skorikov, 1938a:145, unjustified emendation

***Bombus (Rh.) armeniacus* Radoszkowski**

armeniacus Radoszkowski, 1877b:202

***Bombus (Rh.) mesomelas* Gerstaecker**

Agrorum (Schrank, 1781:397 [*Apis*])
arvensis (Gmelin in Linnaeus, 1790:2786 [*Apis*]) unjustified replacement name for *agrorum* Schrank, 1781:397
mesomelas Gerstaecker, 1869:321

○ NOMENCLATURE. Warncke (1986) listed *B. agrorum* (Schrank) as questionably conspecific with *B. distinguendus*, but without any explanation. Although I know of no extant type specimens, Schrank's (1781) description of his *B. agrorum* of 'Habitat ruri' from Austria appears to me to be almost certainly of the same species as *B. mesomelas*, because the head is described as black and the pale hairs of the thorax and of gastral tergum I are described as grey, with the remainder of the gaster rusty or tawny-yellow (the head and the pale pubescence of the thorax and gaster are more uniformly dull yellowish for *B. distinguendus*). See the comments on *B. distinguendus*.

✱ APPLICATION TO ICZN. Although *B. agrorum* is the oldest available name for the present interpretation of this species, the name *B. mesomelas* has been in

common use for the species since 1947 (e.g. Tkalcü, 1969, 1975; Delmas, 1976; Reinig, 1974, 1981; Özbek, 1983; Rasmont, 1983; Ormosa, 1986a, b; Rasmont *et al.*, 1987, 1995). I know of no publications using the name *B. agrorum* (Schrank) since 1947, although the name *B. agrorum* (Fabricius) was in widespread use for another species (= *B. pascuorum*) until Richards (1968). It is suggested that, in the interests of stability (ICZN, 1985: Article 23b), an application be made to ICZN to use its Plenary Power to suppress the unused senior synonym, *B. agrorum*, and its unjustified replacement name, *B. arvensis* (ICZN, 1985: Article 79) (see the comments on *B. muscorum*).

***Bombus (Rh.) pomorum* (Panzer)**

pomorum (Panzer, 1805(86):18 [*Bremus*])
Lefebvrei Lepeletier, 1836:461

**Subgenus KALLOBOMBUS Dalla Torre**

Bombus (Kallobombus) Dalla Torre, 1880:40, type-species *Apis soroensis* Fabricius (= *Bombus soroensis* (Fabricius)) by subsequent designation of Sandhouse, 1943:561

Bombus (Callobombus) Dalla Torre, 1896:503, unjustified emendation

Bombus (Soroensibombus) Vogt, 1911:63, type-species *Apis soroensis* Fabricius (= *Bombus soroensis* (Fabricius)) by monotypy

[*Bombus (Soroensibombus)* Ball, 1914:78, incorrect subsequent spelling]

[*Soroçoënsibombus* Skorikov, 1922a: map 15, incorrect subsequent spelling]

***Bombus (Kl.) soroensis* (Fabricius)**

Cardui (Müller, 1776:165 [*Apis*])
forensis (Fabricius, [1777, see Baker, 1996a:9]:246 [*Apis*])
Proteus Gerstaecker, 1869:325
perplexus Radoszkowski, 1884:82, not of Cresson, 1863:91 (= *B. perplexus* Cresson)
Radoszkowskyi Dalla Torre, 1890:139, replacement name for *perplexus* Radoszkowski, 1884:82
miniatocaudatus Vogt, 1909:56

○ NOMENCLATURE. Baker (1996a) has established

that the name *B. cardui* has narrow priority over *B. soroeensis* by publication date.

✱ APPLICATION TO ICZN. Although *B. cardui* is the oldest available name for the present interpretation of this species, the name *B. soroeensis* has been in common use for the species since 1947 (e.g. Tkalcü, 1969, 1975; Løken, 1973; Alford, 1975; Delmas, 1976; Pekkarinen, 1979; Reinig, 1981; Özbek, 1983; Rasmont, 1983; Ito, 1985; Ormosa, 1986a; Rasmont *et al.*, 1995). The only publications using the name *B. cardui* since 1947 are those of Baker (1996a, b). Using this name contrary to the purpose of priority is not accepted as usage in the sense of the Code (ICZN, 1985: Article 23b), and so cannot justify the continued use of the name *B. cardui* in place of *B. soroeensis*. It is suggested that, in the interests of stability, an application be made to ICZN to use its Plenary Power to suppress the unused senior synonym (ICZN, 1985: Article 79) (see the comments on *B. muscorum*).



Subgenus **ALPINOBOMBUS** Skorikov

Alpinobombus Skorikov, 1914a:123, type-species *Apis alpina* Linnaeus (= *Bombus alpinus* (Linnaeus)) by subsequent designation of Frison, 1927:66

Bombus (*Alpinobombus*) Krüger, 1917:62

Alpinibombus Skorikov, 1937:53, unjustified emendation

COMMENT. Species of the subgenus *Alpinobombus* make up the most northerly distributed of all bee faunas (e.g. K. W. Richards, 1973). Indeed, three of the five species have a nearly circumpolar distribution, as a major component of an Arctic bumble bee fauna (Williams, 1996b). This relative homogeneity of the Arctic fauna among northern continents resembles the pattern in the Arctic flora, which shows little regional differentiation in comparison with more southern floras (Hooker, 1861; Walker, 1995).

Bombus* (AL.) *hyperboreus Schönherr✱

Arctica (Quenzel in Acerbi, 1802:253 [*Apis*])

hyperboreus Schönherr, 1809:57, unjustified replacement name for *arcticus* Quenzel, 1802:253

chydensis Yarrow, 1955:151, examined

● TAXONOMIC STATUS. The identity of *B. arcticus* (Quenzel) has been uncertain. Warncke (1986) listed *B. arcticus* (Quenzel) as conspecific with *B. lapponicus* without any explanation. Presumably this was because *B. lapponicus* is extensively pale on the dorsum, although the pale pubescence is differentiated into yellow and red areas and much of it is much paler than Quenzel's description. I agree with Løken (1973) that, from the original description and the illustration (no type specimen is known to exist), *B. arcticus* (Quenzel) is most likely to be conspecific with *B. hyperboreus*, which has the pale pubescence uniformly brownish yellow.

○ NOMENCLATURE. The name *B. arcticus* has rarely been used for this species in preference to *B. hyperboreus*, and perhaps only as a misidentification of *B. arcticus* Kirby (see e.g. Franklin, 1913; Richards, 1931a). Løken (1973) considered *B. arcticus* (Quenzel) to be a *nomen oblitum*, so she continued to use the name *B. hyperboreus*. However, *nomen oblita* are not supported for a publication of this date by the present Code (ICZN, 1985: Article 79c(iii)), although it does allow that *B. arcticus* (Quenzel) could be suppressed by use of the Plenary Power. See the comments on *B. polaris* Curtis.

✱ APPLICATION TO ICZN. Although *B. arcticus* is the oldest available name for the present interpretation of this species, the name *B. hyperboreus* has been in common use for the species since 1947 (e.g. Løken, 1973; Milliron, 1973a; K. W. Richards, 1973; Svensson & Lundberg, 1977; Hurd, 1979; Pekkarinen, 1979; Pekkarinen *et al.*, 1981; Reinig, 1981; Rasmont, 1983; Pekkarinen & Teräs, 1993). It is suggested that, in the interests of stability (ICZN, 1985: Article 23b), an application be made to ICZN to use its Plenary Power to suppress the unused senior synonym (ICZN, 1985: Article 79), in order to confirm usage of *B. hyperboreus* as the valid name (see the comments on *B. muscorum*).

COMMENT. *B. hyperboreus* has been suggested to be a social parasite in colonies of *B. polaris*, at least facultatively in some parts of its range (Milliron & Oliver, 1966; Løken, 1973; K. W. Richards, 1973). See the comments on *Psithyrus* and *B. inexpectatus*.

Bombus* (AL.) *balteatus Dahlbom✱

balteatus Dahlbom, 1832:36

nivalis Dahlbom, 1832:40

tricolor Dahlbom, 1832:41

?*Kirbiellus* Curtis in Ross, 1835:lxii

kirbyellus Dalla Torre, 1896:527, unjustified emendation

tristis Sparre-Schneider in Friese, 1902:495, not of Seidl, 1837:69 (= *B. humilis* Illiger)

● TAXONOMIC STATUS. *B. balteatus* and *B. kirbiellus* have been considered conspecific by most authors (e.g. Thomson, 1872; Richards, 1931a; Skorikov, 1937;

Pittioni, 1942; Løken, 1973; Hurd, 1979; Thorp *et al.*, 1983), although Milliron (1973a) considered them to be separate species that co-occur in some areas, particularly in Alaska.

Milliron (1973a) described several characters by which to discriminate *B. balteatus* and *B. kirbiellus*, placing particular emphasis on the shape of male gastral sternum VIII and the female malar area.

From the small samples I have examined, I have been unable to find convincing evidence of discrete differences in these characters. Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

○ NOMENCLATURE. Richards (1931a) believed *B. balteatus*, *B. nivalis* and *B. tricolor* to be conspecific and selected the name *B. balteatus* to have precedence because it was published on an earlier page (page priority is not a mandatory part of the Code, only a recommendation, see ICZN, 1985: Recommendation 24A). However, Thomson (1872:35) had already chosen the name *B. nivalis* in precedence to *B. balteatus* and, following the Principle of the First Reviser (ICZN, 1985: Article 24), Thomson's action should now stand. Consequently, the valid name for this species is *B. nivalis*, although the Code (ICZN, 1985) allows that this name could be suppressed by use of the Plenary Power.

✱ APPLICATION TO ICZN. Although *B. nivalis* is the valid name for this species, the name *B. balteatus* has been in common use for the species since 1947 (e.g. Løken, 1973; Milliron, 1973a; Plowright & Stephen, 1973; Hurd, 1979; Pekkarinen, 1979; Reinig, 1981; Rasmont, 1983; Thorp *et al.*, 1983; Laverty & Harder, 1988; Pekkarinen & Teräs, 1993). It is suggested that, in the interests of stability, an application be made to ICZN to use its Plenary Power to suppress the unused name (ICZN, 1985: Article 79) (see the comments on *B. muscorum*). However, the consequence of this action would be that *nivalis* Dahlbom would no longer be available for a subspecies of *B. balteatus*.

Bombus (Al.) neoboreus Sladen

strenuus Cresson, 1863:102, not of Harris, 1776:131 (= *B. lapidarius* (Linnaeus))
neoboreus Sladen, 1919:28

○ NOMENCLATURE. *B. strenuus* Cresson (1863) is a junior secondary homonym in *Bombus* of *Apis strenuus* Harris (1776), and therefore the name *B. strenuus* Cresson is invalid (ICZN, 1985: Article 57c). For this species, the oldest available name is *B. neoboreus*, which becomes the valid name. The only publications using the name *B. strenuus* Cresson since 1947 of which I am aware are by Hurd (1979), Milliron (1973a) and Poole (1996), so this change of valid name is not a serious disruption of common usage.

Bombus (Al.) polaris Curtis✱

Arcticus Kirby in Parry, 1824:ccxvi, examined, not of Quenzel in Acerbi, 1802:253 (= *B. hyperboreus* Schönherr)

Polaris Curtis in Ross, 1835:lxiii, examined
diabolicus Friese, 1911:571
alpiniformis Richards, 1931a:13

○ NOMENCLATURE. Løken (1973) used the name *B. arcticus* Kirby for this species because she considered *B. arcticus* (Quenzel) to be a *nomen oblitum*. However, this is not supported by the present Code for a publication of this date (ICZN, 1985: Article 79c(iii)), although it does allow *B. arcticus* (Quenzel) to be suppressed by use of the Plenary Power. See the comments on *B. hyperboreus*.

✱ APPLICATION TO ICZN. It is suggested above that, in the interests of stability (ICZN, 1985: Article 23b), an application be made to ICZN to use its Plenary Power to suppress *B. arcticus* (Quenzel), the unused senior synonym (ICZN, 1985: Article 79) of *B. hyperboreus*. This would free *B. arcticus* Kirby from junior primary homonymy with *B. arcticus* (Quenzel) (ICZN, 1985: Article 57b), so that it would become the valid name for this species (see the comments on *B. hyperboreus*). However, although the name *B. arcticus* Kirby has been in use for this species (e.g. Løken, 1973; Sakagami, 1976; Svensson & Lundberg, 1977; Reinig, 1981), the more frequently used name has been *B. polaris* (e.g. Milliron & Oliver, 1966; Milliron, 1973a; K.W. Richards, 1973; Hurd, 1979; Pekkarinen, 1979; Pekkarinen *et al.*, 1981; Rasmont, 1983; Pekkarinen & Teräs, 1993). In the interests of stability, the application to ICZN might be extended to suppress *B. arcticus* Kirby, in order to conserve the current usage of *B. polaris* as the valid name.

Bombus (Al.) alpinus (Linnaeus)

alpina (Linnaeus, 1758:579 [*Apis*]) examined



Subgenus *SUBTERRANEOBOMBUS* Vogt

Bombus (*Subterraneobombus*) Vogt, 1911:62, type-species *Apis subterranea* Linnaeus (= *Bombus subterraneus* (Linnaeus)) by subsequent designation of Frison, 1927:68

Subterraneibombus Skorikov, 1938a:145, unjustified emendation

***Bombus* (St.) *melanurus* Lepeletier**

melanurus Lepeletier, 1836:469, examined
?difficillinus Skorikov, 1912:609, examined
subdistinctus Richards, 1928a:333, examined

● TAXONOMIC STATUS. Several of these nominal taxa have been treated as separate species and at least *B. difficillinus* may indeed prove to be a separate species. However, aside from differences in colour pattern, they are closely similar in morphology with a range of variation (Williams, 1991). Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

***Bombus* (St.) *fragrans* (Pallas)**

fragrans (Pallas, 1771:474 [*Apis*])
?mongol Skorikov, 1912:607, examined
?chiarharensis Yasumatsu, 1940:94 (provisional synonym)

● TAXONOMIC STATUS. This taxon is interpreted here in the broadest sense, to include a complex of poorly-known taxa (Williams, 1991). More evidence is awaited.

***Bombus* (St.) *amurensis* Radoszkowski**

Amurensis Radoszkowski, 1862:590, examined

● TAXONOMIC STATUS. I have seen no males of this species and its precise relationships remain unclear.

***Bombus* (St.) *fedtschenkoi* Morawitz**

Fedtschenkoi Morawitz in Fedtschenko, 1875:5

***Bombus* (St.) *personatus* Smith**

personatus Smith, 1879:132, examined
Roborowskyi Morawitz, 1886:197, examined

***Bombus* (St.) *subterraneus* (Linnaeus)**

subterranea (Linnaeus, 1758:579 [*Apis*]) examined
Nemorum (Scopoli, 1763:307 [*Apis*])
?saltuum (Panzer, 1801(75):21 [*Apis*])

○ NOMENCLATURE. Løken (1984) interpreted *B. saltuum* as being conspecific with *B. barbutellus* (see the comments on *B. barbutellus*). Warncke (1986) interpreted *B. saltuum* as having been described from a male (presumably because the antennae were described as rather long) conspecific with *B. subterraneus*. No type specimen is known. The de-

scription of the anterior part of the gaster of *B. saltuum* as ashen and the middle part as nearly bald is perhaps slightly closer to *B. subterraneus*, because although both species may have gastral tergum I with pale hair and terga I–III sparsely haired, this hair is much shorter on *B. subterraneus* and the posterior fringing hairs of the terga often appear greyish-white.

If *B. saltuum* were not accepted as most likely to be conspecific with *B. subterraneus*, then further action would be required. If both interpretations were considered to remain supportable, then it might be considered appropriate (ICZN, 1985: Article 75b) to designate a specimen of *B. subterraneus* as neotype of *Apis saltuum* in order to conserve the current usage of *B. barbutellus*. Alternatively, if *B. saltuum* were considered more likely to be conspecific with *B. barbutellus*, then *B. saltuum* would become the oldest available name for that species, even though the name has not been used in the last 50 years. In the interests of stability (ICZN, 1985: Article 23b), an application could then be made to ICZN to use its Plenary Power to suppress the unused senior synonym (ICZN, 1985: Article 79).

COMMENT. This species has been introduced into New Zealand (e.g. Gurr, 1957; Macfarlane & Gurr, 1995).

***Bombus* (St.) *distinguendus* Morawitz** ♂

nemorum (Fabricius, 1775:382 [*Apis*]) not of Scopoli, 1763:307 (= *B. subterraneus* (Linnaeus)), not of Fabricius, 1775:380 (?= *B. bohemicus* Seidl)
elegans Seidl, 1837:67
distinguendus Morawitz, 1869:32

○ NOMENCLATURE. The name *B. elegans* has been applied to several taxa by different authors. Tkalcü (1969:901–903) reasoned that Seidl had originally described *B. elegans* from an individual of the species that has more recently been known by the name *B. distinguendus*, although Seidl's original type is lost. According to Tkalcü, a specimen of *B. mesomelas* may then have been substituted as the type, but now this cannot be found either. Any remaining confusion could be resolved by the designation of an appropriate neotype. See the comments on *B. mesomelas*.

★ APPLICATION TO ICZN. Although *B. elegans* may be the oldest available name for the present interpretation of this species, the name *B. distinguendus* has been in common use for the species since 1947 (e.g. Tkalcü, 1969, 1974a; Løken, 1973; Alford, 1975; Delmas, 1976; Sakagami, 1976; Pekkarinen, 1979; Reinig, 1981; Pekkarinen *et al.*, 1981; Rasmont, 1983; Pekkarinen & Teräs, 1993; Rasmont *et al.*, 1995). I know of no publications using the name *B. elegans* for this taxon (only for *B. mesomelas* Gerstaecker as a misidentification) since 1947. It is suggested that, in

the interests of stability (ICZN, 1985: Article 23b), and to prevent confusion with *B. mesomelas*, an application be made to ICZN to use its Plenary Power to suppress the unused senior synonym (ICZN, 1985: Article 79) (see the comments on *B. muscorum*).

Bombus (*St.*) *appositus* Cresson
appositus Cresson, 1878:183

Bombus (*St.*) *borealis* Kirby
borealis Kirby, 1837:272



Subgenus *ALPIGENOBOMBUS* Skorikov

Alpigenobombus Skorikov, 1914a:128, type-species *Alpigenobombus pulcherrimus* Skorikov (= *Bombus kashmirensis* Friese) by subsequent designation of Williams, 1991:65

Bombus (*Mastrucobombus*) Krüger, 1917:66, type-species *Bombus mastrucatus* Gerstaecker (= *Bombus wurflenii* Radoszkowski) by monotypy

Bombus (*Alpigenobombus*) Frison, 1927:64

[*Nobilibombus* Skorikov, 1933a:62, published without fixation of type-species]

[*Bombus* (*Nobilibombus*) Bischoff, 1936:12, type-species *Nobilibombus morawitziides* Skorikov (= *Bombus nobilis* Friese) by monotypy, published as a junior synonym]

Alpigenobombus Skorikov, 1938b:1, unjustified emendation

[*Pyrobombus* (*Nobilibombus*) Milliron, 1961:54, type-species *Bombus nobilis* Friese (cited as *Bombus nobilis* Skorikov) by original designation, published as a junior synonym]

Bombus (*Nobilibombus*) Richards, 1968:222, type-species *Bombus nobilis* Friese by original designation (see Williams, 1991)

[*Alpegenobombus* Wang, 1979:188, incorrect subsequent spelling]

- **TAXONOMIC STATUS.** Richards (1968) treated *Alpigenobombus* and *Nobilibombus* as separate subgenera. Following Bischoff (1936), I have treated them as a single subgenus *Alpigenobombus* (Williams, 1991), for which the evidence for monophyly is strong (Williams, 1995).

Bombus (*Ag.*) *kashmirensis* Friese

kashmirensis Friese, 1909[September, Tkalcü, 1974b]:673 examined

stramineus Friese, 1909[September, Tkalcü, 1974b]:673

tetrachromus Cockerell, 1909[November, Tkalcü, 1974b]:397, examined

pulcherrimus (Skorikov, 1914a:128 [*Alpigenobombus*])

- **TAXONOMIC STATUS.** Several of these nominal taxa have been treated as separate species. However, aside from differences in colour pattern, they are closely similar in morphology with a range of variation (Williams, 1991). Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

- **NOMENCLATURE.** Tkalcü (1974b) first regarded *B. kashmirensis* and *B. stramineus* as conspecific and, following the Principle of First Reviser (ICZN, 1985: Article 24), chose *B. kashmirensis* as the name for the species.

Bombus (*Ag.*) *wurflenii* Radoszkowski

Wurflenii Radoszkowski, 1859:482, examined

[*Wurleini* Radoszkowski, 1877b:191, incorrect subsequent spelling]

mastrucatus Gerstaecker, 1869:326, examined

alpigenus Morawitz, 1874:132

Bombus (*Ag.*) *nobilis* Friese

?*validus* Friese, 1905:510, examined (provisional synonym)

nobilis Friese, 1905:513

?*sikkimi* Friese, 1918:82, examined (provisional synonym)

[*morawitziides* Skorikov, 1922a:159, published without description]

[*morawitziides* Skorikov, 1931:203, published without description]

?*morawitziides* (Skorikov, 1933a:62 [*Nobilibombus*]) examined (provisional synonym)

?*xizangensis* Wang, 1979:188, examined (provisional synonym)

chayaensis Wang, 1979:189, examined, **new synonym**

- **TAXONOMIC STATUS.** Several of these nominal taxa have been treated as separate species.

Friese (1905) described *B. validus* initially (p. 510) as having a quadrate malar area and untoothed mandibles, but went on (p. 517) to place it within the *mastrucatus* (= *B. wurflenii*) group, which he characterised as having a short malar area and toothed mandibles. Tkalcü (1987) designated as lectotype of *B. validus* a female with a quadrate malar area and multi-toothed mandibles. He also synonymised *B. morawitziides* with *B. validus*.

The type specimens of *B. nobilis* have also been in some doubt (Richards, 1968). In the same publication

as the description of *B. validus*, Friese (1905) described the female of *B. nobilis* as having a 'quadratisch' malar area and 4–5 teeth on the mandible (even though he placed it [p. 519] in a group with *B. lapidarius*). The original description lists several females (particularly from Sichuan), but the only putative type female that I have been able to examine (although it carries no Friese 'type' label) is in the Berlin museum collection and is a specimen of *B. friseanus* labelled 'Kashgar' (this locality is outside the known distribution range of either *B. nobilis* or *B. friseanus*). The specimen does not match the original description of the mandibles of *B. nobilis* and so cannot be considered a valid syntype. Nonetheless, the identity of *B. nobilis* is clear from the original description, so the designation of a neotype is not justified (ICZN, 1985: Article 75b).

B. chayaensis appears to me to be very closely similar to the yellow banded *B. nobilis* (in the strict sense) and I am unaware of any reason to treat them as separate species.

B. nobilis is interpreted here in the broadest sense, to include a complex of morphologically closely similar taxa (Williams, 1991). At least some of the taxa included may prove to be separate species from *B. nobilis*. The most obvious variation is in the colour of the pale thoracic bands, which may be yellow (*B. nobilis*), yellow-white (*B. sikkimi*), grey-white (*B. morawitzoides*), or almost completely replaced by black (*B. validus*). However, aside from these differences in colour pattern, they are similar in morphology with a range of variation. Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

○ NOMENCLATURE. Following the Principle of First Reviser (ICZN, 1985: Article 24), and as the first author to regard these taxa as conspecific, I select the name *B. nobilis* as the valid name in preference to *B. validus* from the available names for this species from Friese (1905).

***Bombus* (Ag.) *genalis* Friese**

genalis Friese, 1918:84, examined

● TAXONOMIC STATUS. I have seen no males of this species and its precise relationships remain unclear.

***Bombus* (Ag.) *grahami* (Frison)**

grahami (Frison, 1933:334 [*Brenus*])

***Bombus* (Ag.) *breviceps* Smith**

nasutus Smith, 1852a:44, examined

breviceps Smith, 1852a:44, examined

dentatus Handlirsch, 1888:227

simulus Gribodo, 1892:114, examined

orichalceus Friese, 1916:107

rufocognitus Cockerell, 1922:4, examined

pretiosus Bischoff, 1936:11, examined, not of Friese, 1911:571 (= *B. polaris* Curtis)

?*angustus* Chiu, 1948:59 (provisional synonym)

bischoffiellus (Tkalcü, 1977:224 [*Alpigenobombus*]) replacement name for *pretiosus* Bischoff, 1936:11

● TAXONOMIC STATUS. Several of these nominal taxa have been treated as separate species. At least *B. dentatus* [Himalaya] and *B. angustus* [Taiwan] may prove to be separate species (e.g. Tkalcü, 1968b, 1989). However, aside from differences in colour pattern, they are similar in morphology with a range of variation (Williams, 1991). Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

○ NOMENCLATURE. Tkalcü (1968b) first regarded *B. nasutus* and *B. breviceps* as likely to be conspecific and, following the Principle of First Reviser (ICZN, 1985: Article 24), chose *B. breviceps* as the name for the species.



Subgenus **PYROBOMBUS** Dalla Torre

Bombus (*Pyrobombus*) Dalla Torre, 1880:40, type-species *Apis hypnorum* Linnaeus (= *Bombus hypnorum* (Linnaeus)) by monotypy

Bombus (*Poecilobombus*) Dalla Torre, 1882:23, type-species *Bombus sitkensis* Nylander by subsequent designation of Sandhouse, 1943:589

[*Bombus* (*Pyrrhobombus*) Dalla Torre, 1882:28, incorrect subsequent spelling]

Bombus (*Pyrrhobombus*) Dalla Torre, 1896:503, unjustified emendation

Bombus (*Pratobombus*) Vogt, 1911:49, type-species *Apis pratorum* Linnaeus (= *Bombus pratorum* (Linnaeus)) by subsequent designation of Frison, 1927:67

[*Bombus* (*Pratibombus*) Ball, 1914:78, incorrect subsequent spelling]

Bombus (*Anodontobombus*) Krüger, 1917:61,65 (proposed as a section name but stated by Milliron, 1961:53, to be synonymous with his concept of the subgenus *Pyrobombus* Dalla Torre), type-species *Apis hypnorum* Linnaeus (= *Bombus hypnorum* (Linnaeus)) by subsequent designation of Williams, 1991:69

Bombus (Uncobombus) Vogt in Krüger, 1917:65 (proposed as a group name but stated by Milliron, 1961:53, to correspond to his concept of *Pyrobombus* Dalla Torre), type-species *Apis hypnorum* Linnaeus (= *Bombus hypnorum* (Linnaeus)) by subsequent designation of Williams, 1991:69

Bombus (Lapponicobombus) Quilis-Pérez, 1927:19, type-species *Apis lapponica* Fabricius (= *Bombus lapponicus* (Fabricius)) by subsequent designation of Milliron, 1961:58

[*Bombus (Hypnorubombus)* Quilis-Pérez, 1927:19, incorrect original spelling]

[*Bombus (Laponicobombus)* Quilis-Pérez, 1927:63, incorrect original spelling]

Bombus (Hypnorobombus) Quilis-Pérez, 1927:97, type-species *Apis hypnorum* Linnaeus (= *Bombus hypnorum* (Linnaeus)) by monotypy

Pratibombus Skorikov, 1938b:1, unjustified emendation

COMMENT. This is the largest subgenus of *Bombus*. The highest richness of *Pyrobombus* species occurs in the New World (there are no species known from south of Panama), although the earliest-diverging species within the subgenus appear to be in the Old World (Williams, 1991). This is the opposite pattern to that shown by the next-largest subgenus (of social parasites), *Psithyrus* (see the comments on the subgenus *Psithyrus*).

***Bombus (Pr.) abnormis* (Tkalčü)**

abnormis (Tkalčü, 1968a:33 [*Pyrobombus*]) examined

***Bombus (Pr.) hypnorum* (Linnaeus)**

Hypnorum (Linnaeus, 1758:579 [*Apis*]) examined

leucopygus Illiger, 1806:172

calidus Erichson in Middendorff, 1851:65

fletcheri Richards, 1934:90, examined

insularis Sakagami & Ishikawa, 1969:180, not of Smith, 1861:155 (= *B. insularis* (Smith))

koropokkrus Sakagami & Ishikawa, 1972:610, replacement name for *insularis* Sakagami & Ishikawa, 1969:180

● TAXONOMIC STATUS. *B. hypnorum* is a broadly distributed species with a fairly easily recognised brown-black-white colour pattern (e.g. Reinig, 1939; Williams, 1991). Recently, Starr (1992) has described what appears to be a divergent, brownish-black orange-tailed colour form from a disjunct peripheral population on the island of Taiwan.

***Bombus (Pr.) perplexus* Cresson**

perplexus Cresson, 1863:91

***Bombus (Pr.) haematurus* Kriechbaumer**

haematurus Kriechbaumer, 1870:157

***Bombus (Pr.) subtypicus* (Skorikov)**

leucopygus Morawitz in Fedtschenko, 1875:3, not of Illiger,

1806:172 (= *B. hypnorum* (Linnaeus))

[*leucopygus* (Skorikov, 1914b:294 [*Pratobombus*]) incorrect subsequent spelling]

subtypicus (Skorikov, 1914b:294 [*Pratobombus*]) examined

leucurus Bischoff & Hedicke, 1931:391, replacement name for *leucopygus* Morawitz in Fedtschenko, 1875:3

kohistanensis (Tkalčü, 1989:49 [*Pyrobombus*]) examined

***Bombus (Pr.) mirus* (Tkalčü)**

mirus (Tkalčü, 1968a:37 [*Pyrobombus*]) examined

?*tibetanus* Friese, 1913:86, examined, not of Morawitz, 1886:202 (= *B. tibetanus* (Morawitz))

***Bombus (Pr.) lemniscatus* Skorikov**

lemniscatus Skorikov, 1912:607, examined

flavopilosus Friese, 1918:84, examined

peralpinus Richards, 1930:646, examined

***Bombus (Pr.) lepidus* Skorikov**

lepidus Skorikov, 1912:606, examined

genitalis Friese, 1913:85, examined

tetrachromus Friese, 1918:85, examined, not of Cockerell, 1909:397 (= *B. kashmiriensis* Friese)

?*yuennanicola* Bischoff, 1936:7, examined

***Bombus (Pr.) infirmus* (Tkalčü)**

leucurus Bischoff, 1936:8, examined, not of Bischoff & Hedicke, 1931:391 (= *B. subtypicus* (Skorikov))

infirmus (Tkalčü, 1968a:24 [*Pyrobombus*]) replacement name for *leucurus* Bischoff, 1936:8

***Bombus (Pr.) parthenius* Richards**

parthenius Richards, 1934[14 April, Williams & Cameron, 1993]:89, examined

?*sonani* (Frison, 1934[30 April, Williams & Cameron, 1993]:175 [*Bremus*]) examined

?*infrequens* (Tkalčü, 1989:56 [*Pyrobombus*]) examined (provisional synonym)

● TAXONOMIC STATUS. Several of these nominal taxa have been treated as separate species. At least *B. sonani* [Taiwan] and *B. infrequens* [northern Burma to southern China] may prove to be separate species. However, aside from differences in colour pattern, they are closely similar in morphology (Williams, 1991). Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

***Bombus (Pr.) luteipes* Richards**

luteipes Richards, 1934:89, examined

?*avanus* (Skorikov, 1938b:2 [*Pratibombus*]) (provisional synonym)

signifer (Tkalčü, 1989:52 [*Pyrobombus*]), examined

● TAXONOMIC STATUS. The identity of *B. avanus*

is in doubt because the type cannot be found. The description of the colour pattern resembles *B. parthenius* and *B. luteipes*, and the description of the longer than usual squama (= gonostylus) and the half-crooked apex of the sagitta (= penis valve) appear to be closely similar to *B. luteipes*, so these taxa are very likely to be conspecific. More evidence is awaited.

***Bombus* (Pr.) *flavescens* Smith**

flavescens Smith, 1852a:45, examined

mearnsi Ashmead, 1905:959

bagnionensis Cockerell, 1920:631, **new synonym**

tahanensis Pendlebury, 1923:65, examined

?*rufoflavus* Pendlebury, 1923:66, examined (provisional synonym)

● **TAXONOMIC STATUS.** Several of these nominal taxa have been treated as separate species. *B. rufoflavus* [Peninsular Malaysia] and *B. bagnionensis* [Philippines] are particularly distinct in colour pattern. They may prove to be separate species, but from the material available from a few sites, they appear to me to be closely similar in morphology to *B. flavescens* (Williams, 1991). Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

***Bombus* (Pr.) *rotundiceps* Friese**

rotundiceps Friese, 1916:108, examined

montivolanooides Sakagami & Yoshikawa, 1961:431

shillongensis (Tkalčú, 1974b:334 [Pyrobombus]) examined

***Bombus* (Pr.) *beaticola* (Tkalčú)**

beaticola (Tkalčú, 1968a:28 [Pyrobombus]) examined

***Bombus* (Pr.) *picipes* Richards**

flavus Friese, 1905:517, examined, not of Pérez, 1884:265

(= *B. campestris* (Panzer))

picipes Richards, 1934:90, examined

klapperichi Pittioni, 1949:266, examined

?*nikiforuki* Tkalčú, 1961b:354 (provisional synonym)

● **TAXONOMIC STATUS.** *B. nikiforuki* was described from a single worker from Qinghai. From the description, it appears to be closely similar to *B. picipes* and is likely to be conspecific.

○ **NOMENCLATURE.** With *Psithyrus* regarded as being a subgenus of the genus *Bombus* (Williams, 1991, 1995), *B. pratorum* subsp. *flavus* Friese (1905) becomes a junior secondary homonym in *Bombus* of *Psithyrus campestris* var. *flavus* Pérez (1884) (deemed to be subspecific, see ICZN, 1985: Article 45g(ii)), and therefore the name *B. flavus* Friese is invalid (ICZN, 1985: Article 57c). For this species, the oldest available name of which I am aware is *B. parthenius*

var. *picipes* Richards, 1934 (deemed to be subspecific, see ICZN, 1985: Article 45g(ii)), which becomes the valid name, *B. picipes*. The only publications using the name *B. flavus* Friese since 1947 of which I am aware are by Sakagami (1972), Ito (1993) and Yao & Luo (1997), so this change of valid name is not a serious disruption of common usage.

***Bombus* (Pr.) *ardens* Smith**

ardens Smith, 1879:133, examined

andreae Friese, 1910:405, examined

***Bombus* (Pr.) *modestus* Eversmann**

modestus Eversmann, 1852:134

Baikalensis Radoszkowski, 1877b:203

nymphe Skorikov, 1910b:409

eversmanni Skorikov, 1910c:581, not infrasubspecific after Skorikov, 1922a:149

***Bombus* (Pr.) *cingulatus* Wahlberg**

cingulatus Wahlberg, 1854:208

COMMENT. The distribution of *B. cingulatus* according to Reinig (1939) is shown in Fig. 10.

?*Bombus* (Pr.) *oceanicus* Friese

oceanicus Friese, 1909:675, examined

oceanicus Friese & Wagner, 1910:52, redescribed

● **TAXONOMIC STATUS.** *B. oceanicus* is known only from the Kurile Islands. A particularly close relationship with the otherwise broadly distributed *B. cingulatus* (absent from the Kuriles, but present in Kamchatka. Reinig, 1939; Ito & Sakagami, 1980; Fig. 10) has been suggested by Ito & Sakagami (1980) and it is possible that they are conspecific. More evidence is awaited.

***Bombus* (Pr.) *brodmannicus* Vogt**

Brodmannicus Vogt, 1909:49, examined

***Bombus* (Pr.) *pratorum* (Linnaeus)**

pratorum (Linnaeus, 1761:424 [*Apis*]) examined

COMMENT. This species was deliberately introduced into Sydney, Australia, although it is not known to have persisted (Olliff, 1895). Until the twentieth century, *B. pratorum* was not known from Ireland, where it is now well established (see references in Alford, 1975, 1980) (see comments on *B. monticola*).

***Bombus* (Pr.) *jonellus* (Kirby)**

Jonella (Kirby, 1802:338 [*Apis*]) examined

alboanalis Franklin, 1913:385

● **TAXONOMIC STATUS.** *B. alboanalis* has been regarded both as a separate species (Franklin, 1913; Frison, 1927) and as conspecific with either *B. frigidus* (Burks, 1951; Hurd, 1979; Poole, 1996) or *B. jonellus* (Williams, 1991 [as *B. jonellus* from western Canada]; Scholl *et al.*, 1995).

Recently, Scholl *et al.* (1995) concluded from studies of enzyme mobility morphs that whereas *B. alboanalis* and *B. frigidus* have separate gene pools, in contrast, *B. alboanalis* and *B. jonellus* show a low level of genetic differentiation. They also noted the lack of colour gradation between sympatric *B. alboanalis* and *B. frigidus*.

From the limited amount of material I have examined, I believe that *B. alboanalis* and *B. jonellus* are morphologically closely similar. Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

***Bombus (Pr.) pyrenaeus* Pérez**☼

pyrenaeus Pérez, [1880, see Baker, 1996d:300]:127, not of Lepeletier, 1832:375 (= *B. rupestris* (Fabricius))
tenuifasciatus Vogt, 1909:49
 [pyreneus Pagliano, 1995:23, incorrect subsequent spelling]

○ **NOMENCLATURE.** With *Psithyrus* regarded as being a subgenus of the genus *Bombus* (Williams, 1991, 1995), *B. pyrenaeus* Pérez (1880) becomes a junior secondary homonym in *Bombus* of *Psithyrus pyrenaeus* Lepeletier (1832), and therefore the name *B. pyrenaeus* Pérez is invalid (ICZN, 1985: Article 57c). The next available name, *tenuifasciatus*, was used by Vogt (1909) for individuals with particular colour patterns from both *B. pyrenaeus* Pérez and *B. sichelii*. The choice of which of these two homonyms should have precedence depends on the Principle of the First Reviser (ICZN, 1985: Article 24). As far as I have been able to discover, Tkalcü (1973:266) is the first author to have recognised this problem. He recognised precedence for *B. pyrenaeus* ssp. *tenuifasciatus* Vogt. Consequently, the oldest available name for this species, and therefore the valid name, is *B. tenuifasciatus*.

☼ **APPLICATION TO ICZN.** Although *B. tenuifasciatus* is the oldest available name for this species, the name *B. pyrenaeus* has been in common use for the species since 1947 (e.g. Krusemen, 1958; Tkalcü, 1969, 1973, 1975; Reinig, 1972, 1981; Delmas, 1976; Rasmont, 1983; Ornos, 1986; Williams, 1991; Rasmont *et al.*, 1995). It is suggested that, in the interests of stability, an application be made to ICZN to use its Plenary Power to suppress the senior homonym (ICZN, 1985: Article 79) (see the comments on *B. muscorum*). However, the consequence of this action

would be that *pyrenaeus* (Lepeletier) would no longer be available for a subspecies of *B. rupestris*.

***Bombus (Pr.) biroi* Vogt**

biroi Vogt, 1911:51, examined
nursei Friese, 1918:84, examined
 ?*agnatus* Skorikov, 1933b:248, examined, not of Skorikov, 1912:97 (= *B. monticola* Smith)
 ?*kotzschii* Reinig, 1940:227, examined

● **TAXONOMIC STATUS.** Several of these nominal taxa have been treated as separate species. However, aside from differences in colour pattern, they are closely similar in morphology with a range of variation (Williams, 1991). Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

***Bombus (Pr.) frigidus* Smith**

frigidus Smith, 1854:399, examined

***Bombus (Pr.) sandersoni* Franklin**

sandersoni Franklin, 1913:353

***Bombus (Pr.) flavifrons* Cresson**☼

pleuralis Nylander, 1848:231, examined
flavifrons Cresson, 1863:105, new synonym

● **TAXONOMIC STATUS.** *B. pleuralis* and *B. flavifrons* were regarded as separate species by Franklin (1913), and Poole (1996) also lists them as separate species, without explanation. In my opinion, the lectotype of *B. pleuralis* designated by Milliron (1960:95) is an individual of the dark form of *B. flavifrons* (see descriptions of variation by e.g. Stephen, 1957; Thorp *et al.*, 1983). See also the comments on *B. mixtus*.

○ **NOMENCLATURE.** *B. pleuralis* is the oldest available name for this species.

☼ **APPLICATION TO ICZN.** Although *B. pleuralis* is the oldest available name for the present interpretation of this species, the name *B. flavifrons* has been in common use for the species since 1947 (e.g. Stephen, 1957; Thorp, 1969, 1970; Plowright & Stephen, 1973; Macior, 1975; Sakagami, 1976; Hurd, 1979; Plowright & Owen, 1980; Thorp *et al.*, 1983; Lavery & Harder, 1988). I know of no publications using the name *B. pleuralis* since 1947, apart from the list by Poole (1996). It is suggested that, in the interests of stability (ICZN, 1985: Article 23b), an application be made to ICZN to use its Plenary Power to suppress the unused senior synonym (ICZN, 1985: Article 79) (see the

comments on *B. muscorum*). However, the consequence of this action would be that *pleuralis* would no longer be available for a species or for a subspecies of *B. flavifrons*.

***Bombus* (Pr.) *centralis* Cresson**
centralis Cresson, 1864:41

***Bombus* (Pr.) *vandykei* (Frison)**
vandykei (Frison, 1927:375 [*Bremus*])
cascadensis (Milliron, 1970a:382 [*Pyrobombus*])

***Bombus* (Pr.) *caliginosus* (Frison)**
caliginosus (Frison, 1927:376 [*Bremus*])

***Bombus* (Pr.) *vagens* Smith**
vagens Smith, 1854:399, examined

***Bombus* (Pr.) *mixtus* Cresson**☼
Praticola Kirby, 1837:274
mixtus Cresson, 1878:186, not of Kriechbaumer, 1870:160
(= *B. maxillosus* Klug), new synonym

● TAXONOMIC STATUS. The identity of *B. praticola* has remained uncertain (e.g. Cresson, 1863; Franklin, 1913). Recently, Poole (1996) has listed *B. praticola*, *B. mixtus* and *B. flavifrons* as separate species without explanation.

Although I know of no type material, Kirby provided a description of *B. praticola* from northern Canada (latitude 65° North) with a colour pattern (including anterior half of abdomen yellow, posterior ferruginous) that for individuals from this area is most likely to be conspecific either with *B. mixtus* (some individuals have few black hairs on gastral terga II–III), or with *B. flavifrons* (which has terga V–VI black, although this is not always apparent from the dorsal view). In his original description of *B. flavifrons*, Cresson (1863) conceded that this might be the same species as Kirby's *B. praticola*, and he went on to write (p. 106) that he had not yet identified *B. praticola*. Franklin (1913:371) wrote that he had 'been unable to decide whether the original description of *B. praticolus* [sic] referred to this species [*B. flavifrons*] or to the colour variant of *pleuralis* [intermediate colour patterns between *B. flavifrons* and *B. pleuralis*]' Milliron (1971:42) subsequently listed *Pyrobombus praticola flavifrons* (Cr.) as a member of his 'Praticola Group'.

However, here I follow R. Miller (*in litt.*), who believes that the original material was more likely to have been of the species that has come to be known as *B. mixtus*. See the comments on *B. flavifrons*.

○ NOMENCLATURE. *B. praticola* is probably the oldest available name for this species. Any remaining

confusion could be resolved by the designation of an appropriate neotype (e.g. see the comments on *B. subterraneus*).

☼ APPLICATION TO ICZN. Although *B. praticola* is probably the oldest available name for this species, the name *B. mixtus* has been in common use for the species since 1947 (e.g. Stephen, 1957; Thorp, 1970; Plowright & Stephen, 1973; K. W. Richards, 1973; Macior, 1975; Sakagami, 1976; Hurd, 1979; Plowright & Owen, 1980; Thorp *et al.*, 1983; Lavery & Harder, 1988; Macfarlane *et al.*, 1994). It is suggested that, in the interests of stability, an application be made to ICZN to use its Plenary Power to suppress the senior synonym and homonym (ICZN, 1985: Article 79) (see the comments on *B. muscorum*). However, the consequence of this action would be that *mixtus* (Kriechbaumer) would no longer be available for a subspecies of *B. maxillosus*.

***Bombus* (Pr.) *sitkensis* Nylander**
Sitkensis Nylander, 1848:235

***Bombus* (Pr.) *melanopygus* Nylander**
melanopyge Nylander, 1848:236
Edwardsii Cresson, 1878:184
melanopygus Handlirsch, 1888:231, unjustified emendation
[*melanopygus* Viereck, 1904:99, incorrect subsequent spelling]
melanopygus Franklin, 1913:334, justified emendation

● TAXONOMIC STATUS. *B. melanopygus* and *B. edwardsii* were shown by Owen & Plowright (1980) to differ principally by a single allele controlling the colour of the pubescence on gastral terga II–III. There can be little doubt that they are conspecific.

***Bombus* (Pr.) *lapponicus* (Fabricius)**
lapponica (Fabricius, 1793:318 [*Apis*])
?sylvicola Kirby, 1837:272
zhaosu Wang, 1985:162, examined, new synonym

● TAXONOMIC STATUS. *B. sylvicola* is morphologically closely similar to *B. lapponicus*, and it has been suggested repeatedly that they may be conspecific (e.g. Sladen, 1919; Skorikov, 1922a, 1937; Pittioni, 1942, 1943; Thorp, 1962; Thorp *et al.*, 1983).

B. zhaosu was described from material from Xinjiang, China, and is closely similar to *B. lapponicus*.

These three nominal taxa have been treated as separate species. However, aside from differences in colour pattern, they are closely similar in morphology. Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

?*Bombus* (Pr.) *monticola* Smith

montanus Smith, 1844:549, not of Lepeletier, 1836:463 (= *B. ruderarius* (Müller))

monticola Smith, 1849:lx, replacement name for *montanus* Smith, 1844:549

lugubris Sparre-Schneider, 1909:155, not of Kriechbaumer, 1870:159 (= *B. maxillosus* (Klug))

scandinavicus Friese, 1912:684, replacement name for *lugubris* Sparre-Schneider, 1909:255

● **TAXONOMIC STATUS.** *B. scandinavicus* (= *B. monticola*) and *B. lapponicus* are names that were applied initially to two colour forms in Scandinavia.

Løken (1973) reported that these two taxa overlap narrowly in distribution and intergrade. However, they have been found to differ consistently (for samples analysed) in the composition of cephalic secretions (Bergström & Svensson, 1973; Svensson & Bergström, 1977). Svensson (1973, 1979) also described subtle differences in morphological characters, although other morphological studies by Løken (1973) and Pekkarinen (1979) found no distinct differences. Pekkarinen (1982, *in litt.*) now believes that they are separate species.

It remains possible that there is a hybrid zone where the colour forms intergrade, with some gene flow. In this case, depending on the species concept embraced, these taxa might be considered conspecific (see the comments on *B. ruderatus*). Until further evidence is available, I shall continue to treat them as separate species.

COMMENT. Until the twentieth century *B. monticola* was not known from Ireland, where it is now established (see references in Alford, 1975, 1980) (see comments on *B. pratorum*).

***Bombus* (Pr.) *bimaculatus* Cresson**

bimaculatus Cresson, 1863:92

***Bombus* (Pr.) *impatiens* Cresson**

impatiens Cresson, 1863:90

***Bombus* (Pr.) *vosnesenskii* Radoszkowski**

Vosnesenskii Radoszkowski, 1862:589

***Bombus* (Pr.) *bifarius* Cresson**

bifarius Cresson, 1878:185

andamanus Gribodo, 1882:268, examined

fernaldi Franklin, 1911:157, not a replacement name

● **TAXONOMIC STATUS.** *B. andamanus* was described as originating from 'Andaman' (= Andaman Islands, Indian Ocean), but appears to be a mislabelled queen of *B. bifarius* from western North America (Tkalci, 1966). I have examined this specimen and agree with this identification (i.e. contrary to Richards, 1929*b*, it is not a species of the subgenus *Bombus* s. str.).

***Bombus* (Pr.) *huntii* Greene**

Huntii Greene, 1860:172

***Bombus* (Pr.) *ternarius* Say**

ternarius Say, 1837:414

ornatus Smith, 1854:398, examined

***Bombus* (Pr.) *ephippiatus* Say**

ephippiatus Say, 1837:414

formosus Smith, 1854:403, examined

lateralis Smith, 1879:134, examined

?*wilmattae* Cockerell, 1912:21, examined

?*alboniger* Franklin, 1915:409, examined

folsoni (Frisson, 1923:322 [*Brennus*]) examined

● **TAXONOMIC STATUS.** *B. wilmattae*, *B. alboniger* and *B. ephippiatus* have been regarded both as conspecific and as separate species. Recently, *B. wilmattae* and *B. ephippiatus* were regarded as separate species by Labougle *et al.* (1985) and Labougle (1990), who described diagnostic characters of colour pattern and morphology. However, D. Yanega (*in litt.*) and G. Chavarría (pers. com.) believe that all of these nominal taxa are part of the widespread and variable *B. ephippiatus*. Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

B. folsoni was described as originating from 'Kina Bala / N. Borneo' (= Gunung Kinabalu, Sabah), but appears to be a mislabelled queen of *B. ephippiatus*, probably from Costa Rica or Panama (Starr, 1989). I have examined this specimen and agree with this identification.

**Subgenus *FESTIVOBOMBUS* Tkalci**

[*Atrocinctob.[ombus]* Skorikov, 1933*b*:244, published without description]

Pyrobombus (*Festivobombus*) Tkalci, 1972:26, type-species *Bombus festivus* Smith by original designation

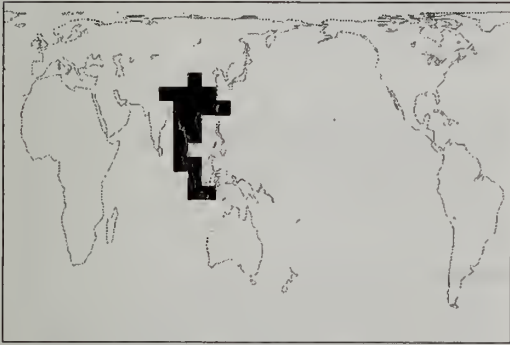
Bombus (*Festivobombus*) Williams, 1985*b*:240

● **TAXONOMIC STATUS.** Richards (1968) treated *B. atrocinctus* (= *B. festivus*) as a species of the

subgenus *Pyrobombus*, even though this required numerous exceptions in the diagnosis. I have followed Tkalcü(1972, 1974b) in treating *Festivobombus* and *Pyrobombus* as separate subgenera (Williams, 1991), because together they do not form a monophyletic group (Williams, 1995).

***Bombus* (Fs.) *festivus* Smith**

festivus Smith, 1861:152, examined
atrocinctus Smith in Horne, 1870:193, examined
terminalis Smith in Horne, 1870:193, examined



Subgenus *RUFIPEDIBOMBUS* Skorikov

Rufipedibombus Skorikov, 1922a:156, type-species
Bombus rufipes Lepeletier by monotypy
Bombus (*Rufipedibombus*) Richards, 1930:638
Bombus (*Rufipedobombus*) Kruseman, 1952:102, unjustified emendation

***Bombus* (Rf.) *rufipes* Lepeletier**

rufipes Lepeletier, 1836:473
richardsi (Frison, 1930:6 [*Bremus*])

***Bombus* (Rf.) *eximius* Smith**

eximius Smith, 1852b:47, examined
latissimus Friese, 1910:405



Subgenus *PRESSIBOMBUS* Frison

Bremus (*Pressibombus*) Frison, 1935:342, type-species

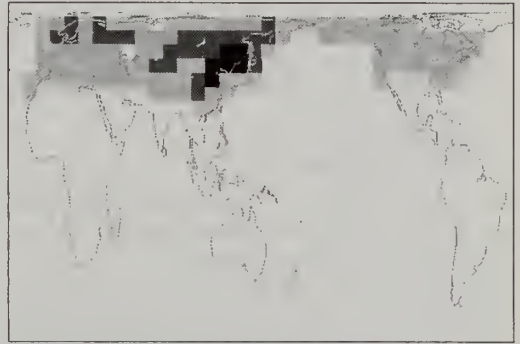
Bremus pressus Frison (= *Bombus pressus* (Frison)) by original designation

Bombus (*Pressobombus*) Kruseman, 1952:102, unjustified emendation

Bombus (*Pressibombus*) Richards, 1968:217

***Bombus* (Pe.) *pressus* (Frison)**

pressus (Frison, 1935:342 [*Bremus*])



Subgenus *BOMBUS* in the strict sense

Bombus (*Leucobombus*) Dalla Torre, 1880:40, type-species *Apis terrestris* Linnaeus (= *Bombus terrestris* (Linnaeus)) by subsequent designation of Sandhouse, 1943:564

Bombus (*Terrestribombus*) Vogt, 1911:55, type-species *Apis terrestris* Linnaeus (= *Bombus terrestris* (Linnaeus)) by subsequent designation of Frison, 1927:67

***Bombus* (Bo.) *sporadicus* Nylander**

sporadicus Nylander, 1848:233
malaisei Bischoff, 1930:4

***Bombus* (Bo.) *tunicatus* Smith**

tunicatus Smith, 1852a:43, examined
vallestris Smith, 1878:8
gilgitensis Cockerell, 1905:223, examined

***Bombus* (Bo.) *franklini* (Frison)**

franklini (Frison, 1921:147 [*Bremus*])

● **TAXONOMIC STATUS.** This species has been treated as conspecific with *B. occidentalis* (= *B. terricola*) by Milliron (1971), but has since been shown to be very distinct in morphology by Plowright & Stephen (1980) and Williams (1991), and in enzyme mobilities by Scholl, Thorp & Obrecht (1992).

COMMENT. *B. franklini* has one of the narrowest distributions of any bumble bee species world-wide. All recent specimens have been collected within a 60 mile (38 km) radius of Grants Pass, Oregon (Thorp, 1970; Thorp *et al.*, 1983).

Bombus (Bo.) affinis* Cressonaffinis* Cresson, 1863:103***Bombus (Bo.) ignitus* Smith***ignitus* Smith, 1869:207, examined*terminalis* Smith, 1873:206, examined, not of Smith in Horne, 1870:193 (= *B. festinus* Smith)*japonicus* Dalla Torre, 1890:139, replacement name for *terminalis* Smith, 1873:206***Bombus (Bo.) terrestris* (Linnaeus)***terrestris* (Linnaeus, 1758:578 [*Apis*])*Audax* (Harris, 1776:130 [*Apis*]) not of Harris, 1776:137 (= *Anthophora* sp.)*canariensis* Pérez, 1895:191*maderensis* Erlandsson, 1979:191

● TAXONOMIC STATUS. *B. terrestris*, *B. maderensis* and *B. canariensis* have been regarded both as conspecific and as separate species.

Erlandsson (1979) argued that the dark individuals from the Canary Islands, previously placed within *B. terrestris* by for example Krüger (1954, 1956), are a separate species, *B. canariensis*. Erlandsson also argued that individuals from the island of Madeira, previously placed within *B. terrestris* by Bischoff (1937), are a separate species, *B. maderensis*. In both cases the morphological characters used to support these distinctions are not strongly divergent from the broad variation within *B. terrestris* in the broad sense. Rasmont (1984) regarded these three taxa as separate species, but Pekkarinen & Kaarnama (1994) treated them as conspecific.

Recent work by Estoup *et al.* (1996) has found that although European mainland populations do not vary significantly among themselves in mitochondrial genes, all island populations studied (from six Mediterranean islands in addition to *B. canariensis*) show significant differences from the mainland populations.

Consequently, viewing these three nominal taxa as separate species may be one interpretation, but this appears to depend on adopting a species concept that admits little colour, morphological or genetic variation within a species and regards current geographical isolation as highly indicative. I prefer to regard these taxa as conspecific until further evidence is available.

○ NOMENCLATURE. Day (1979) described how none of the admissible syntypes of *A. terrestris* Linnaeus is in agreement with the current usage of the name.

To reaffirm the traditional usage of this particularly widely used name, a case was made to ICZN by Løken *et al.* (1994). This sought an Opinion from ICZN (ICZN, 1996) that set aside, by use of its Plenary Power (ICZN, 1985: Articles 78b, 79), the lectotype designation for *A. terrestris* by Day from application

of the Code (ICZN, 1985), and then designated a neotype (ICZN, 1996: 64) to conserve the traditional usage of the name for even the narrowest concept of the taxon (ICZN, 1985: Article 75).

COMMENT. This species has been introduced into New Zealand (e.g. Gurr, 1957; Macfarlane & Gurr, 1995) (see the comments on *B. hortorum*, *B. ruderatus*, and *B. subterraneus*), Tasmania (Cardale, 1993), and Japan (I. Washitani, *in litt.*). It was also apparently introduced into mainland Australia (New South Wales) without persisting (W. Froggatt in Franklin, 1913).

Bombus (Bo.) hypocrita* Pérezhypocrita* Pérez, 1905:30***Bombus (Bo.) patagiatus* Nylander***patagiatus* Nylander, 1848:234*vasilievi* Skorikov, 1913:172***Bombus (Bo.) lucorum* (Linnaeus)***lucorum* (Linnaeus, 1761:425 [*Apis*]), examined*?cryptarum* (Fabricius, 1775:379 [*Apis*])*?modestus* Cresson, 1863:99, not of Eversmann, 1852:134 (= *B. modestus* Eversmann)*?moderatus* Cresson, 1863:109, replacement name for *modestus* Cresson, 1863:99*monozonus* Friese, 1909:674*?magnus* Vogt, 1911:56*?jacobsoni* Skorikov, 1912:610, examined*?burjaeticus* Krüger, 1954:277*?florilegus* Panfilov, 1956:1334*?reinigi* Tkalcü, 1974b:322, examined

● TAXONOMIC STATUS. These bees have received particularly close attention by authors describing the minutiae of colour variation, using at least 186 classical names (see the introduction). At least some of these nominal taxa have been regarded as separate species by some authors (e.g. Rasmont, 1983, 1984, 1988; Scholl & Obrecht, 1983; Scholl *et al.*, 1990; Scholl, Thorp & Obrecht, 1992; Rasmont *et al.*, 1995; Amiet, 1996; Özbek, 1997; Pamilo *et al.*, 1997). In contrast, *B. cryptarum* and the North American *B. moderatus* have recently been treated as conspecific with *B. lucorum* by Poole (1996).

There are conflicting patterns of variation among some characters of these taxa, which are not fully understood (Pekkarinen, 1979; Pamilo *et al.*, 1984; Amiet, 1996; Pamilo *et al.*, 1997). As far as I can tell from the evidence available at present, separation of the taxa for mapping is still not reliable, at least in some areas of their distribution, and particularly in Central and Eastern Asia, where there appears to be a broad range of variation with some intergradation of character combinations (Williams, 1991). Therefore,

because complete mapping of separate taxa is not yet possible for me, *B. lucorum* is interpreted here in the broadest sense, to include a complex of similar taxa. However, these taxa require more critical work to clarify population patterns of variation and inheritance, even in relatively well known areas such as Britain.

○ NOMENCLATURE. When Day (1979) came to fix the application of *A. terrestris* Linnaeus (see the comments on *B. terrestris*), he had no reason to believe that Linnaeus had not described this taxon from the syntype specimen that was subsequently described as the lectotype (= *A. cryptarum* Fabricius, see Rasmont, 1988:52, ?= *B. lucorum* (Linnaeus)). This action brought *B. lucorum* (Linnaeus) into subjective junior synonymy with *B. terrestris* (Linnaeus).

To reaffirm the traditional usage of *B. terrestris* and *B. lucorum*, a case was made to ICZN by Løken *et al.* (1994). This sought an Opinion from ICZN (ICZN, 1996) that set aside, by use of its Plenary Power (ICZN, 1985: Articles 78b, 79), the lectotype designation for *A. terrestris* by Day from application of the Code (ICZN, 1985), and then designated a neotype (ICZN, 1996: 64) to conserve the traditional usage of *B. terrestris* and *B. lucorum* (ICZN, 1985: Article 75).

COMMENT. This species occurs in Iceland, where it has probably been introduced (Prŷs-Jones *et al.*, 1981) (see the comments on *B. hortorum*).

***Bombus (Bo.) terricola* Kirby**

Terricola Kirby, 1837:273

?*occidentalis* Greene, 1858:12

● TAXONOMIC STATUS. *B. terricola* and *B. occidentalis* have been regarded both as conspecific (e.g. Milliron, 1971; Poole, 1996) and as separate species (e.g. Franklin, 1913 [but see p. 239]; Stephen, 1957; Thorp *et al.*, 1983; Scholl *et al.*, 1990).

Many specimens from the north west of North America show a reduction in the extent of the yellow bands on gastral terga II and III, with an expansion of the pale pubescence on tergum IV, and so appear to be intermediate or recombinant individuals. Indeed, Stephen's (1957:74) figure 4 shows several patterns that could represent a continuum of variation between the two forms. Furthermore, Thorp *et al.* (1983: fig. 140a) illustrate individuals of '*B. occidentalis*' from California that look very similar to eastern *B. terricola*. In view of this, Stephen's conclusion that there is no intergradation may result from adopting colour criteria (identifying *B. terricola* in the strict sense either by completely black pubescence of female terga V–VI [p. 15] and male tergum IV [p. 19], or by completely yellow pubescence of tergum II [pp. 19, 71], two character states that do not always occur together, even

in the east) that could be considered as essentially arbitrary points on a continuum (see the comments on *B. fervidus*).

In view of the existence of apparent intermediates between these nominal taxa in at least part of their range, they are treated here as likely to be conspecific. Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.



Subgenus **CULLUMANOBOMBUS** Vogt

Bombus (Cullumanobombus) Vogt, 1911:57, type-species

Apis cullumana Kirby (= *Bombus cullumanus* (Kirby)) by subsequent designation of Frison, 1927:66

Bremus (Rufocinctobombus) Frison, 1927:78, type-species *Bombus rufocinctus* Cresson by monotypy

Cullumanibombus Skorikov, 1938a:145, unjustified emendation

***Bombus (Cu.) rufocinctus* Cresson**

rufocinctus Cresson, 1863:106

***Bombus (Cu.) cullumanus* (Kirby)**

Cullumana (Kirby, 1802:359 [*Apis*]) examined *serrisquama* Morawitz, 1888:224

Silantjewi Morawitz, 1892:132

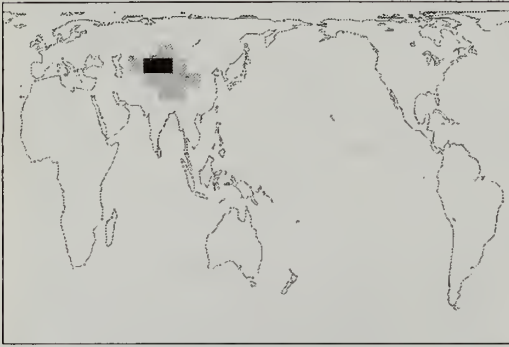
apollineus Skorikov, 1910b:412

● TAXONOMIC STATUS. Several of these nominal taxa have been treated as separate species. However, aside from differences in colour pattern, they are closely similar in morphology (Panfilov, 1951). Rasmont (1988) has drawn attention to the co-occurrence of the white-banded *B. apollineus* with the yellow-banded *B. serrisquama* in northern Iran, apparently without intermediate individuals. But by analogy, it is possible that this colour difference could be the effect of a single allele for pigment (cf. *B. melanopygus*, see also the comments on *B. keriensis*). Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

***Bombus (Cu.) unicus* Morawitz**
unicus Morawitz, 1883:235
controversus Skarikov, 1910b: 411

● TAXONOMIC STATUS. *B. unicus* is similar to *B. cullumanus* and could possibly be conspecific. However, the male genitalia appear to be more distinct (Panfilov, 1951) from those of the other taxa traditionally considered subspecies of *B. cullumanus*.

***Bombus (Cu.) semenoviellus* Skorikov**
semenoviellus Skorikov, 1910b:410



nominal taxa should not be considered conspecific.



Subgenus **OBERTOBOMBUS** Reinig

Bombus (Obertobombus) Reinig, 1930:107, type-species
Bombus oberti Morawitz by monotypy
[*Obertibombus* Skorikov, 1931:239, incorrect subsequent spelling]
Bombus (Obertibombus) Reinig, 1934:167, unjustified emendation

● TAXONOMIC STATUS. Richards (1968) treated *Obertobombus* as a synonym of the subgenus *Sibiricobombus*. I have recognised *Obertobombus* and *Sibiricobombus* as separate subgenera, because together they do not form a monophyletic group (Williams, 1995).

***Bombus (Ob.) morawitzi* Radoszkowski**
Morawitzi Radoszkowski, 1876:101, examined
hydrophthalmus Morawitz, 1883:240, examined

***Bombus (Ob.) oberti* Morawitz**
Oberti Morawitz, 1883:238, examined
Semenovi Morawitz, 1886:198, examined
xionglaris Wang, 1982:432, examined, **new synonym**
duanjiaoris Wang, 1982:444, examined
zhadaensis Wang, 1982:444, examined, **new synonym**

● TAXONOMIC STATUS. *B. xionglaris* and *B. zhadaensis* are closely similar to *B. oberti* in morphology and in colour pattern. These bees occur at high altitudes and are not common in collections (Williams, 1991). However, I know of no reason why these

Subgenus **MELANOBOMBUS** Dalla Torre

Bombus (Melanobombus) Dalla Torre, 1880:40, type-species *Apis lapidaria* Linnaeus (= *Bombus lapidarius* (Linnaeus)) by subsequent designation of Sandhouse, 1943:569

Bombus (Lapidariobombus) Vogt, 1911:58, type-species *Apis lapidaria* Linnaeus (= *Bombus lapidarius* (Linnaeus)) by subsequent designation of Sandhouse, 1943:562

Kozlovibombus Skorikov, 1922a:152, type-species *Bombus kozlovi* Skorikov, 1910b (= *Bombus keriensis* Morawitz) in the sense of Skorikov, 1922a (based on males = *Bombus pyrosoma* Morawitz, a misidentification, see Reinig, 1934:169, requiring designation by ICZN), by subsequent fixation of Sandhouse, 1943:561

Bombus (Kozlovibombus) Bischoff, 1936:10, unjustified emendation

Lapidariobombus Skorikov, 1938a:145, unjustified emendation

?*Bombus (Tanguicobombus)* Pittioni, 1939d:201, type-species *Bombus tanguiticus* Morawitz by original designation (provisional synonym)

[*Bombus (Lapedariobombus)* Esmaili & Rastegar, 1974:52, incorrect subsequent spelling]

***Bombus (Ml.) tanguiticus* Morawitz**
tanguiticus Morawitz, 1886:200

● TAXONOMIC STATUS. Queens of *B. tanguiticus* are morphologically very distinctive (discussed in Williams, 1991), so much so that Pittioni (1939d) considered the species warranted a subgenus of its own. The male remains apparently unknown (the species occurs at high altitudes in Tibet [= Xizang] and is very rare in collections), so that its precise relationships are difficult to resolve at present and a separate subgenus seems premature.

***Bombus (Ml.) simillinus* Smith**
simillinis Smith, 1852b:48, examined
[*similis* Smith, 1854:403, incorrect subsequent spelling]
[*simillinus* Dalla Torre, 1896:548, incorrect subsequent spelling]
grossiventris Friese, 1931:303, examined

oculatus (Frison, 1933:335 [*Bremus*]) examined
tonsus (Skorikov, 1933b:248 [*Sibiricobombus*]) examined
simillimus Williams, 1991:99, justified emendation

***Bombus* (Ml.) *richardsiellus* (Tkalcü)**

richardsiellus (Tkalcü, 1968a:42 [*Pyrobombus*]) examined

***Bombus* (Ml.) *pyrosoma* Morawitz**

pyrosoma Morawitz, 1890:349, examined
pyrrhosoma Dalla Torre, 1896:544, unjustified emendation
wutaishanensis (Tkalcü, 1968a:39 [*Pyrobombus*]) examined

● TAXONOMIC STATUS. *B. pyrosoma* has been considered conspecific with *B. friseanus* (Bischoff, 1936) and has been considered conspecific with *B. formosellus*, *B. friseanus* and *B. flavothoracicus* (= *B. miniatus*) (Williams, 1991). From a preliminary analysis of colour variation, S.-f. Wang and J. Yao report (*in litt.*) that these taxa appear to remain discrete and are likely to be separate species. More evidence is awaited.

?*Bombus* (Ml.) *formosellus* (Frison)

formosellus (Frison, 1934:163 [*Bremus*]) examined

● TAXONOMIC STATUS. *B. formosellus* has been considered conspecific with *B. pyrosoma*, *B. friseanus* and *B. flavothoracicus* (= *B. miniatus*) (Williams, 1991), as a disjunct peripheral population on Taiwan. From a preliminary analysis of colour variation, S.-f. Wang and J. Yao report (*in litt.*) that these taxa appear to remain discrete and are likely to be separate species. More evidence is awaited.

?*Bombus* (Ml.) *friseanus* Skorikov

friseanus Skorikov, 1933a:62, examined
hönei Bischoff, 1936:10, examined

● TAXONOMIC STATUS. *B. friseanus* has been considered conspecific with *B. pyrosoma* (Bischoff, 1936; Tkalcü, 1961b; Sakagami, 1972) and has been considered conspecific with *B. pyrosoma*, *B. formosellus* and *B. flavothoracicus* (= *B. miniatus*) (Williams, 1991). From a preliminary analysis of colour variation, S.-f. Wang and J. Yao report (*in litt.*) that these taxa appear to remain discrete and are likely to be separate species. More evidence is awaited.

?*Bombus* (Ml.) *miniatus* Bingham

flavothoracicus Bingham, 1897:552, examined, not of Hoffer, 1889:49 (= *B. campestris* (Panzer))
miniatus Bingham, 1897:553, examined
eurythorax Wang, 1982:435, examined, **new synonym**

stenothorax Wang, 1982:439, examined, **new synonym**

● TAXONOMIC STATUS. *B. miniatus* has been considered conspecific with *B. pyrosoma*, *B. formosellus* and *B. friseanus* (Williams, 1991).

Evidence of intermediates between *B. miniatus* and *B. friseanus* is not strong, but not least because so little material is available from where these taxa occur in close proximity in the eastern Himalaya. The few workers and males from this area that I have seen are difficult to assign to either taxon with any confidence, although the queens are closer to the colour pattern of *B. miniatus* (Williams, 1991). More evidence is awaited.

B. eurythorax and *B. stenothorax* are closely similar in morphology and colour pattern to *B. miniatus*. I know of no reason why these nominal taxa should not be considered conspecific.

○ NOMENCLATURE. With *Psithyrus* regarded as being a subgenus of the genus *Bombus*, *B. flavothoracicus* Bingham (1897) becomes a junior secondary homonym in *Bombus* of *Psithyrus campestris* var. *flavothoracicus* Hoffer (1889) (deemed to be subspecific, see ICZN, 1985: Article 45g(ii)), and therefore the name *B. flavothoracicus* Bingham is invalid (ICZN, 1985: Article 57c).

For this species, the oldest available name is *B. miniatus*, which becomes the valid name. The only subsequent publications of which I am aware that use the name *B. flavothoracicus* for this taxon as a species are by Tkalcü (1974b), Wang (1982) and Macior (1990), so this change of valid name is not a serious disruption of common usage.

***Bombus* (Ml.) *rufofasciatus* Smith**

rufo-fasciatus Smith, 1852b:48, examined
Prsiewalskyi Morawitz, 1880:342
rufocinctus Morawitz, 1880:343, examined, not of Cresson, 1863:106 (= *B. rufocinctus* Cresson)
chinensis Dalla Torre, 1890[June 25]:139, replacement name for *rufocinctus* Morawitz, 1880:343; not of Morawitz, 1890[April 30]:352 (= *B. chinensis* (Morawitz))
waterstoni Richards, 1934:88, examined

***Bombus* (Ml.) *ladakhensis* Richards**

ladakhensis Richards, 1928a:336, examined, not infrasubspecific after Tkalcü, 1974b:335
phariensis Richards, 1930:642, examined, not infrasubspecific after Tkalcü, 1974b:336
variopictus Skorikov, 1933b:248, examined
reticulatus Bischoff, 1936:7, examined

***Bombus* (Ml.) *semenovianus* (Skorikov)**

semenovianus (Skorikov, 1914a:127 [*Lapidariobombus*]) examined

***Bombus (ML.) incertus* Morawitz**
incertus Morawitz, 1881:229

***Bombus (ML.) lapidarius* (Linnaeus)**
Lapidaria (Linnaeus, 1758:579 [*Apis*]) examined
Strenuus (Harris, 1776:131 [*Apis*]) examined
eriophorus Klug, 1807:265, examined
caucasicus Radoszkowski, 1859:482, examined

***Bombus (ML.) keriensis* Morawitz**
keriensis Morawitz, 1886:199, examined
separandus Vogt, 1909:61, examined
kohli Vogt, 1909:61, examined, not of Cockerell, 1906:75
 (= *B. morio* (Swederus))
kozlovi Skorikov, 1910b:413, replacement name for *kohli*
 Vogt, 1909:61
tenellus Friese, 1913:86
 [*alagesianus* (Skorikov, 1922a:152 [*Lapidariobombus*])
 published without description]
alagesianus Reinig, 1930:89
richardsi Reinig, 1935:341, not of Frison, 1930:6 (= *B.*
rufipes Lepeletier)
tibetensis Wang, 1982:439, replacement name for *richardsi*
 Reinig, 1935:341
trilineatus Wang, 1982:441, examined, **new synonym**

● **TAXONOMIC STATUS.** Several of these nominal taxa have been treated as separate species (e.g. Skorikov, 1931), although *B. keriensis* has also long been considered a broadly-distributed and variable species, including both yellow-banded and white-banded individuals throughout much of its range (Reinig, 1935, 1939; Williams, 1991; Fig. 9).

B. trilineatus is morphologically closely similar to *B. keriensis*. I know of no reason why these nominal taxa should not be considered conspecific.

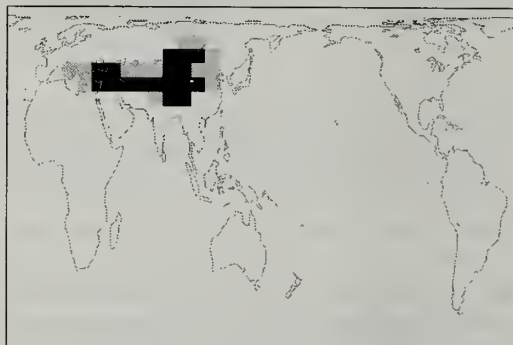
***Bombus (ML.) sichelii* Radoszkowski**
Sichelii Radoszkowski, 1859:481, examined
 [*Sicheli* Radoszkowski, 1877b:213, incorrect subsequent spelling]
tenuifasciatus Vogt, 1909:49, not of Vogt, 1909:49 (= *B.*
pyrenaicus Pérez) after Tkalcü, 1973:266
chinganicus Reinig, 1936:6, not of Reinig, 1936:8 (?= *B.*
bohemicus Seidl)
erzurumensis (Özbek, 1990:209 [*Pyrobombus*]) examined,
new synonym

● **TAXONOMIC STATUS.** Until recently, the white-banded form of *B. sichelii* has been known from west of the Caspian Sea only from the Caucasus (Reinig, 1935). Now that *B. erzurumensis* (morphologically closely similar to *B. sichelii*-*

i and with white bands) has been described from Turkey, it could be interpreted as another white-banded, western colour form. By analogy (cf. comments on *B. melanopygus*), the difference in colour could be the

effect of a single allele for pigment.

Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.



Subgenus *SIBIRICOBOMBUS* Vogt

Bombus (*Sibiricobombus*) Vogt, 1911:60, type-species *Apis sibirica* Fabricius (= *Bombus sibiricus* (Fabricius)) by subsequent designation of Sandhouse, 1943:599
Sibiricobombus Skorikov, 1938a:145, unjustified emendation
 [*Bombus* (*Sibericobombus*) Kruseman, 1952:101, incorrect subsequent spelling]

***Bombus (Sb.) sibiricus* (Fabricius)**
fibrica (Fabricius, 1781:478 [*Apis*]) examined
flaviventris Friese, 1905:514, examined, **new synonym**
ochrobasis Richards, 1930:655, examined, **new synonym**

● **TAXONOMIC STATUS.** *B. sibiricus* and *B. flaviventris* have been regarded as separate species. Females of *B. flaviventris* are morphologically closely similar to those of *B. sibiricus*, but differ in having the orange pubescence dorsally between the wing bases and on gastral terga IV–VI replaced with black. S.-f. Wang and J. Yao have kindly shown me the male of *B. flaviventris*, which is closely similar in its genitalia to *B. sibiricus*.

B. ochrobasis appears to differ from *B. flaviventris* only in the lighter hue of the yellow pubescence of *B. ochrobasis*.

At present I know of no good biological reason why these three nominal taxa should not be regarded as conspecific. More evidence is awaited.

COMMENT. *B. flaviventris* has long been placed in the subgenus *Subterraneobombus* (e.g. Skorikov, 1922a; Richards, 1930, 1968), although the characters of the females (Williams, 1991) and the males (Wang & Yao, unpublished) agree with the species of the subgenus *Sibiricobombus*.

***Bombus (Sb.) obtusus* Richards**
obtus Richards, 1951:196, examined

***Bombus (Sb.) asiaticus* Morawitz**

- asiatica* Morawitz in Fedtschenko, 1875:4, examined
longiceps Smith, 1878:8
Regeli Morawitz, 1880:337, examined
regelii Dalla Torre, 1896:544, unjustified emendation
[*miniato-caudatus* Vogt, 1909:50, infrasubspecific]
miniato-caudatus Vogt, 1911:61, examined, not of Vogt,
1909:56 (= *B. soroensis* (Fabricius))
heicens Wang, 1982:430, examined, **new synonym**
huangcens Wang, 1982:430, examined, **new synonym**
flavicollis Wang, 1985:163, examined, **new synonym**
baichengensis Wang, 1985:164, examined, **new synonym**

● **TAXONOMIC STATUS.** Several of these nominal taxa have been treated as separate species.

B. heicens, *B. huangcens*, *B. flavicollis* and *B. baichengensis* are morphologically closely similar to *B. asiaticus* and differ only in details of the colour pattern. In the case of the yellow unbanded colour form and the grey banded colour form in Kashmir (Fig. 12), there is evidence of interbreeding, with many recombinant individuals in some localities (Williams, 1991).

Aside from differences in colour pattern, these taxa are similar in morphology with a range of variation (Williams, 1991). Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

***Bombus (Sb.) niveatus* Kriechbaumer**

- niveatus* Kriechbaumer, 1870:158
?*vorticoides* Gerstaecker, 1872:290, examined (provisional synonym)

● **TAXONOMIC STATUS.** *B. niveatus* and *B. vorticoides* have been regarded both as conspecific (Schmiedeknecht, 1883; Handlirsch, 1888; Dalla Torre, 1896; Schulz, 1906) and, more recently, as separate species (e.g. Skorikov, 1922a; Pittioni, 1938; Tkalcü, 1969; Reinig, 1981; Rasmont, 1983).

As far as I am aware, the white-banded *B. niveatus* occurs only within the broader distributional bounds of the yellow-banded *B. vorticoides* (within its 'extent of occurrence' in the sense of Gaston, 1994). Although they differ in the colour of the pale pubescence (Pittioni, 1939a), they are closely similar in morphology (Williams, 1991; Baker, 1996b). Pittioni (1938) and Baker (1996b) report that they occur at different altitudes, without intermediate colour forms. However, the significance of this is unclear, because Baker (1996b) notes that the white-banded *B. niveatus* co-occurs with other bumble bees (*B. apollineus* (= *B. cullumanus*), *B. simulatilis* (= *B. ruderarius*)) that also show strong convergences in these areas towards the white-banded colour pattern, while elsewhere they are more broadly distributed in yellow-banded colour forms. By analogy with other species (cf. comments

on *B. melanopygus*, *B. keriensis*), the difference in colour could be the effect of a single pair of alleles for pigment. It is suspicious that both colour forms show identical variation in the extent of pale fringes to the pubescence on the posterior of tergum II.

Until more evidence for differences between these nominal taxa other than colour is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

***Bombus (Sb.) sulfureus* Friese**

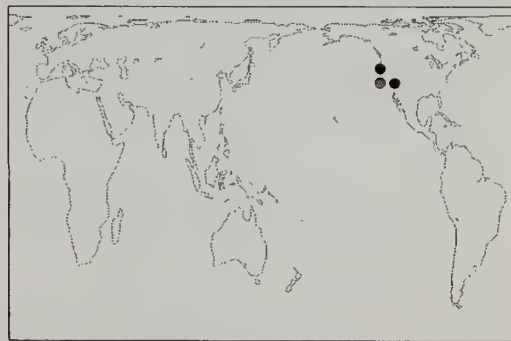
- sulfureus* Friese, 1905:521, examined

**Subgenus *FRATERNOBOMBUS* Skorikov**

- Alpigenobombus* (*Fraternobombus*) Skorikov, 1922a:156,
type-species *Apathus fraternus* Smith (= *Bombus fraternus* (Smith)) by subsequent designation of Frison,
1927:63
Bombus (*Fraternobombus*) Franklin, 1954:44

***Bombus (Fr.) fraternus* (Smith)**

- fraternus* (Smith, 1854:385 [*Apathus*]) examined

**Subgenus *CROTCHIIBOMBUS* Franklin**

- Bombus* (*Crotchiibombus*) Franklin, 1954:51, type-species *Bombus crotchii* Cresson by original designation

Bombus (Cr.) crotchii* CressonCrotchii* Cresson, 1878:184**Subgenus *ROBUSTOBOMBUS* Skorikov***Volucellobombus* Skorikov, 1922a:149, type-species*Bombus volucelloides* Gribodo (?= *B. melaleucus* Handlirsch) by monotypy*Alpigenobombus* (*Robustobombus*) Skorikov, 1922a:157, type-species *Bombus robustus* Smith by subsequent designation of Sandhouse, 1943:597*Bombus* (*Robustobombus*) Richards, 1968:217

COMMENT. Variation within and among the species of this subgenus is particularly poorly understood and a critical review is urgently needed.

Bombus (Rb.) melaleucus* Handlirschmelaleucus* Handlirsch, 1888:228, examined*?volucelloides* Gribodo, 1892:119 (provisional synonym)*?vogti* Friese, 1903:254 (provisional synonym)*?nigrothoracicus* Friese, 1904:188, examined (provisional synonym)*melanoleucus* Schulz, 1906:267, unjustified emendation

● TAXONOMIC STATUS. Several of these nominal taxa have been treated as separate species.

B. volucelloides is closely similar to *B. melaleucus*, but has been considered to be a separate species (e.g. Milliron, 1973b). *B. vogti* is also closely similar to *B. volucelloides*, and these two taxa have been considered both as conspecific (e.g. Franklin, 1913; Labougle, 1990) and as separate species (e.g. Milliron, 1973b). G. Chavarría (pers. com.) also believes that *B. melaleucus*, *B. volucelloides* and *B. vogti* are all conspecific.

In addition, it seems to me that *B. nigrothoracicus* is more likely to be conspecific with *B. vogti* than with *B. ecuadorius* (see the comments on *B. ecuadorius*).

Thus *B. melaleucus* is interpreted here in a very broad sense, to include much variation that is not yet well understood. Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

○ NOMENCLATURE. For this species, the oldest available name of which I am aware is *B. melaleucus*, which becomes the valid name. The name *B. volucelloides* has been in most common use, although for just part of this species. However, it seems premature to conserve *B. volucelloides* by suppressing *B. melaleucus* until the taxa are better understood, because the name *B. melaleucus* might yet be required for a separate species or subspecies.

Bombus (Rb.) ecuadorius* MeunierEcuadorius* Meunier, 1890:66*?butteli* Friese, 1903:254, examined (provisional synonym)

● TAXONOMIC STATUS. *B. butteli* is closely similar to *B. ecuadorius*. They have been considered to be separate species (e.g. Franklin, 1913; Milliron, 1973b), although Franklin conceded that *B. butteli* (which has grey hairs intermixed on the thoracic dorsum) might be 'only a variety or subspecies' of *B. ecuadorius* (which has the thoracic dorsum entirely black).

B. ecuadorius females are very rare in collections. For example, Milliron (1973b) had seen only five putative specimens (as opposed to 42 specimens of *B. butteli*). Of these five specimens, four were females, and just one was a male, which is the same specimen as the holotype of *B. nigrothoracicus* (see the comments on *B. melaleucus*). This male is labelled 'Bolivia / ?Peru', whereas the rest of Milliron's *B. ecuadorius* are from Ecuador, with the exception of one queen from 'Peru' (it carries no further locality data). This putative male of *B. ecuadorius* differs from the females in having yellow hairs intermixed on the front and rear of the thorax. This was not mentioned in the original description of this male (under the name *B. nigrothoracicus*) by Friese (1904), which Franklin (1913) used subsequently as the sole basis for associating the male with *B. ecuadorius*.

Currently I favour another possible interpretation. This views the male holotype of *B. nigrothoracicus* instead as a semi-melanic male of *B. melaleucus* (the males of *B. volucelloides* [= *B. melaleucus*] that I have seen have the thoracic dorsum extensively yellow). This might explain the difference in colour pattern and distribution of this male from other *B. ecuadorius*. However, a consequence of this interpretation would be that the only remaining known difference between *B. ecuadorius* and *B. butteli* would be in colour pattern, because the main morphological justification for regarding them as separate species (the broader apical process of the gonostylus of the putative male *B. ecuadorius*, now *B. melaleucus* in the broad sense) would have been removed. Further evidence is awaited.

***Bombus (Rb.) robustus* Smith**
robustus Smith, 1854:400, examined

? ***Bombus (Rb.) hortulanus* Friese**
hortulanus Friese, 1904:188, examined
 [*hortukans* Frison, 1925a:155, incorrect subsequent spelling]

● **TAXONOMIC STATUS.** *B. robustus* and *B. hortulanus* have been considered both as conspecific (e.g. Franklin, 1913; Frison, 1925a; G. Chavarría, pers. com.) and as separate species (e.g. Milliron, 1973b; Asperen de Boer, pers.com.).

B. robustus and *B. hortulanus* are morphologically similar. Among the specimens I have seen, individuals that have the sides of gastral terga I–II yellow (*B. robustus*) also have pubescence extending to the middle or almost to the middle of tergum I, and the males have the space between the inner basal process of the gonostylus and the inner apical process narrower than the apical process. Conversely, individuals with the sides of terga I–II black (*B. hortulanus*) have at least the medial third of tergum I hairless, and the space between the inner processes of the male gonostylus is wider than the breadth of the apical process.

Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as separate species.

***Bombus (Rb.) tucumanus* Vachal**
tucumanus Vachal, 1904:10



Subgenus **SEPARATOBOMBUS** Frison
Brenus (*Separatobombus*) Frison, 1927:64, type-species
Bombus separatus Cresson (= *Bombus griseocollis* (DeGeer)) by original designation
Bombus (*Separatobombus*) Franklin, 1954:44

***Bombus (Sp.) morrisoni* Cresson**
Morrisoni Cresson, 1878:183

***Bombus (Sp.) griseocollis* (DeGeer)**
griseo-collis (DeGeer, 1773:576 [*Apis*])
separatus Cresson, 1863:165



Subgenus **FUNEHBOMBUS** Skorikov
Alpigenobombus (*Funebribombus*) Skorikov, 1922a:157,
 type-species *Bombus funebris* Smith by monotypy
Bombus (*Funebribombus*) Richards, 1968:214

***Bombus (Fn.) funebris* Smith**
funebris Smith, 1854:400, examined

***Bombus (Fn.) rohweri* (Frison)**
rohweri (Frison, 1925a:144 [*Brenus*])

● **TAXONOMIC STATUS.** *B. funebris* and *B. rohweri* have been regarded both as conspecific (Milliron, 1962) and as separate species (Frison, 1925a; Asperen de Boer, 1993a; G. Chavarría, pers. com.). They have been distinguished with reference to subtle morphological characters as well as to the consistently and strongly differing colour patterns. Both Asperen de Boer (1993a) and G. Chavarría (pers. com.) found that they co-occur at some localities without intermediate colour patterns. Further evidence is awaited.



Subgenus **BRACHYCEPHALIBOMBUS** Williams
Bombus (*Brachycephalibombus*) Williams, 1985b:247,
 type-species *Bombus brachycephalus* Handlirsch by
 original designation

● TAXONOMIC STATUS. *B. brachycephalus* was not explicitly placed in any subgenus by Richards (1968). I described a separate subgenus *Brachycephalibombus* for *B. brachycephalus* and *B. haueri* (Williams, 1985b), in order to maintain monophyletic groups (Williams, 1995).

***Bombus* (Br.) *brachycephalus* Handlirsch**

brachycephalus Handlirsch, 1888:244

neotropicus (Frison, 1928:151 [*Bremus*])

krusemani Asperen de Boer, 1990:1, examined, new synonym

● TAXONOMIC STATUS. The description of *B. krusemani* shows that this nominal taxon, known from a single location, diverges slightly in colour pattern from the otherwise widespread, common and variable Central American species, *B. brachycephalus*. The information available at present for *B. krusemani* is consistent with the known range of variation within *B. brachycephalus* (e.g. Labougle, 1990). Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

***Bombus* (Br.) *haueri* Handlirsch**

Haueri Handlirsch, 1888:234

COMMENT. Franklin (1913) and Labougle (1990) believed that this species is closely related to *B. crotchii* (although Labougle had not examined any males). Surprisingly, Milliron (1973b) placed *B. haueri* in his 'Dentatus-group', without explanation (*B. dentatus* is a junior synonym of the Indo-Chinese *B. breviceps* of the subgenus *Alpigenobombus*). Possibly Milliron, at least, may have been influenced by Skorikov (1922a), who placed *B. haueri* in the subgenus *Alpigenobombus* (as *Alpigenobombus* (*Alpigenobombus*) *haueri*, which he also listed next to *Ag. (Ag.) crotchii*). However, both sexes of species of the subgenus *Alpigenobombus*, as it has been accepted recently (Richards, 1968; Williams, 1991), are easily distinguished from any New World bumble bees because they have more teeth on the mandibles.

I have examined the morphology of both sexes and, on the basis of cladistic analysis, have grouped *B. haueri* with *B. brachycephalus* (Williams, 1985b, 1995) and with *B. rubicundus* (Williams, 1995). Further evidence is awaited.



Subgenus **RUBICUNDOBOMBUS** Skorikov

Fervidobombus (*Rubicundobombus*) Skorikov, 1922a:154,
type-species *Bombus rubicundus* Smith by subsequent
designation of Sandhouse, 1943:597

Bombus (*Rubicundobombus*) Richards, 1968:217

***Bombus* (Rc.) *rubicundus* Smith**

[*Napensis* Spinola in Osculati, 1850:201, published without description]

rubicundus Smith, 1854:400, examined



Subgenus **COCCINEOBOMBUS** Skorikov

Alpigenobombus (*Coccineobombus*) Skorikov, 1922a:157,
type-species *Bombus coccineus* Fries by subsequent
designation of Sandhouse, 1943:539

Bombus (*Coccineobombus*) Richards, 1968:214

***Bombus* (Cc.) *coccineus* Fries**

coccineus Fries, 1903:254, examined

***Bombus* (Cc.) *baeri* Vachal**

Baeri Vachal, 1904:10



Subgenus **DASYBOMBUS** Labougle & Ayala

Bombus (*Dasybombus*) Labougle & Ayala, 1985:49, type-species *Bombus macgregori* Labougle & Ayala by original designation

● TAXONOMIC STATUS. *B. handlirschi* was not explicitly placed in any subgenus by Richards (1968), and *B. macgregori* had yet to be described. I have grouped *B. handlirschi* with *B. macgregori* in the subgenus *Dasybombus* (Williams, 1995).

Bombus (*Ds.*) *macgregori* Labougle & Ayala
macgregori Labougle & Ayala, 1985:50, examined
menchuae Asperen de Boer, 1995:47, examined, **new synonym**

● TAXONOMIC STATUS. *B. menchuae* was described from a single location and, on the basis of the worker and male I have examined, appears to diverge from *B. macgregori* only in colour pattern. Until more evidence to the contrary is available from critical studies of patterns of variation, I shall treat them as parts of a single variable species.

Bombus (*Ds.*) *handlirschi* Friese
handlirschi Friese, 1903:255, examined

COMMENT. Franklin (1913) believed that this species is closely related to *B. rubicundus*. Milliron (1973*b*) knew 'of no closely related species in the Western Hemisphere'. I have examined the morphology of both sexes and, on the basis of cladistic analysis, have grouped *B. handlirschi* with *B. macgregori* as sister species (Williams, 1995).

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